AN ASSESSMENT OF THE USE OF THE JACKASS PENGUIN AS A SAMPLER OF THE MARINE ENVIRONMENT

by

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ABSTRACT

In this thesis the use of the jackass penguin *Spheniscus demersus* as a sampler of the marine environment is assessed. Between February 1987 and July 1988, 638 monthly diet samples were obtained from adult jackass penguins at west- (Marcus and Jutten Islands) and southwest-coast (Dyer Island) colonies off South Africa, supplementing data collected since 1980. Penguin diet was compared over time and between colonies in order to establish the presence or absence of qualitative changes or quantified trends in the biology of pelagic schooling fish species important to the South African purse-seine fishery, viz. anchovy *Engraulis capensis*, pilchard *Sardinops ocellatus*, maasbanker *Trachurus trachurus* and red-eye *Etrumeus whiteheadii*. The principal prey of jackass penguins and major contributor to commercial catches is anchovy and, consequently, the biology of this fish species was emphasized. Monthly and annual trends in prey composition and anchovy size-range were related to the availability, abundance and distribution of the penguins' prey species in the marine environment.

Frequency of occurrence of prey species was analyzed statistically using a generalized linear model. Frequency of abundance was analyzed graphically by correspondence analysis. Size-frequency distributions and median lengths were analyzed statistically using a chi-square test for differences in probabilities, and two- and multisample median tests, respectively.

Long-term trends in the diet of jackass penguins on the west coast of South Africa were described and interpreted. Trends in monthly probability of occurrence of prey species in penguin diet indicated that the occurrence of alternate prey species to anchovy was dependent on the presence/absence of anchovy. Occurrence and variation in the timing of the annual anchovy migration was reflected in trends of monthly anchovy size-range. Monthly absolute abundance of prey species other than anchovy did not vary seasonally. Annual probability of occurrence and relative numerical abundance of anchovy in penguin diet appeared to reflect high levels of recruitment and an increase in biomass, respectively. At annual time scales, different prey species were

predominant in different years. Based on comparisons of diet- and fishery-based trends in annual abundance, increased stock sizes of prey species were identified. A significant decrease in the size of anchovy taken by jackass penguins between 1980-88 was observed.

The diet of jackass penguins at the west and southwest coast of South Africa during 1980-82 was compared. Comparisons of the last two years are emphasized. Diet samples from penguins at both coasts did not differ significantly in prey composition. Anchovy was the principal prey species at both localities but dominated penguin diet to a greater extent at the southwest than at the west coast. During 1987-88 differences in frequency of occurrence were observed. Absolute abundance of prey species other than anchovy did not vary seasonally in penguin diet at the southwest coast. Anchovy taken by southwest coast penguins were consistently larger and less variable in size than those at the west coast. Penguin diet was shown to reflect general anchovy distribution and migration patterns. Limited local anchovy recruitment occurred at the southwest coast in 1987, but appeared to be at a much smaller scale than that at the west coast. Decreases in the size of anchovy taken by penguins at both coasts were coincident.

Quantified trends in the occurrence and abundance of small anchovy in west-coast penguin diet between 1981-88 were used to determine the timing and strength of anchovy recruitment. Timing was highly variable and late recruitment did not appear to result in reproductive failure of anchovy. Unusual spawning dates were observed. Penguin diet reflected regional but not local changes in recruit biomass. Using the present approach, jackass penguins cannot be used to estimate the strength of anchovy recruitment early in the fishing season.

The use of the jackass penguin as a sampler of the marine environment appears to be limited largely to anchovy stocks. Penguins can be used to obtain information on anchovy populations that may complement other studies and information, on which advice for the management of this important renewable resource is currently based.

GENERAL INTRODUCTION

Birds have received much attention as animals reflecting environmental change (Morrison 1986). Although their use as direct indicators of specific changes in the environment has been described as "tenuous at best" (Morrison 1986), the value of birds as indirect monitors of the environment has clearly been established (Diamond & Filion 1987).

Seabirds are abundant, conspicuous, and easily studied, and tend to feed in the upper trophic levels of marine food webs (Furness & Monaghan 1987). As such, Ashmole & Ashmole (1968), for example, suggested using food samples from seabirds in the study of seasonal variation in the surface fauna of tropical oceanic areas. As samplers of the marine environment, seabirds not only appear to be monitors of marine pollution (Furness 1987, Gilbertson *et al.* 1987), but they may also provide useful information about marine ecosystem structure and dynamics (eg. Croxall 1987), and living marine resources such as pelagic schooling fish (Furness 1987).

It is well known that seabirds exploit shoals of pelagic fish (Brown 1980). Several seabirds are thus natural predators of commercially exploited fish species (Furness & Ainley 1984), and several studies have demonstrated relationships between variables of seabird biology and fish stocks important to fisheries (eg. Crawford & Shelton 1978, Hunt & Butler 1980, Anderson *et al.* 1980, 1982; Monaghan & Zonfrillo 1986). Recently, seabird feeding ecology and commercial fisheries relationships have received considerable attention (eg. Nettleship *et al.* 1984, Berruti 1987, Duffy *et al.* 1987a, Walter *et al.* 1987). Hislop & Harris (1985) were able to show correlations between the frequency of sprats *Sprattus sprattus* fed to young puffins *Fratercula arctica* on the Isle of May, and modified VPA (Virtual Population Analysis) estimates of the total biomass of sprats in the North Sea. Furthermore, indices of the abundance of overwintering larval herring *Clupea harengus* in the North Sea in February correlated positively with the annual frequencies of herring in the diet of puffins (Hislop & Harris 1985).

Although most studies did not test the use of seabirds as fish stock indicators explicitly (Berruti & Colclough (1987) being an exception), they suggest that monitoring of relevant seabird parameters could provide an indication of the state of fish stocks. Berruti (1985) extended this argument by proposing that variables of seabird biology, such as feeding ecology, breeding biology and population dynamics, not only provide fish stock indices, but may yield additional information useful to fisheries managers. For example, studies of the foraging ecology of seabirds may be used to assess population dynamics and behaviour of pelagic schooling fish, as well as allow inferences to be made about specific parameters of the biology of their prey (Berruti 1987). Hatch (1984) inferred spatial and temporal changes in the availability of prey of rhinoceros auklets *Cerorhinca monocerata*, tufted *F. cirrhata* and horned *F. corniculata* puffins in the Gulf of Alaska. Vermeer & Westrheim (1984) investigated the diet of rhinoceros auklets on the coast of British Columbia. They concluded *inter alia*, as did Sunada *et al.* (1981), that seabird diet may be useful in monitoring age-classes of certain fish species.

In the southern Benguela upwelling region off the southwest coast of Africa, Cape anchovy *Engraulis capensis* and South African pilchard *Sardinops ocellatus* are the dominant pelagic fishes (Bergh *et al.* 1985). The Cape cormorant *Phalacrocorax capensis*, jackass penguin *Spheniscus demersus* and Cape gannet *Morus capensis* at present make up 45.5, 27.8 and 19.4 % of the total resident breeding seabird biomass in the southern Benguela, respectively (Duffy *et al.* 1987b). Avifaunal studies designed to assist in the management of renewable resources, especially pelagic schooling fish, in the Benguela upwelling ecosystem have therefore concentrated on these three seabird species (Berruti *et al.* 1989). For example, examination of population parameters of Cape cormorants, jackass penguins and Cape gannets allowed an investigation of the distribution of anchovy on the west coast of the Cape province during the 1982-83 "warm event" (Duffy *et al.* 1984).

Seabird diet has played a key role in providing qualitative, as well as quantitative, data on the distribution, behaviour and abundance of certain fish species in the southern Benguela ecosystem (eg. Duffy *et al.* 1985, Armstrong *et al.* 1987, Berruti 1987, Duffy *et al.* 1987c, Walter *et al.* 1987). Jackson (1988) has shown that during the day white-chinned petrels *Procellaria aequinoctialis* and sooty shearwaters *Puffinus griseus*, which are surface or near-surface feeders, fed on prey presently regarded as mesopelagic. Berruti & Colclough (1987) established the use of Cape gannet diet as a reliable monitor of the trend in pilchard stocks at low biomass.

Principles guiding the choice of seabirds providing potentially useful advice to fisheries management exist (Anon. 1982; Berruti 1985, 1987). Following Berruti (1985), the biology of jackass penguins complies with several of these. Firstly, jackass penguin diet contains a significant proportion of the commercially exploited fish species, dominated by anchovy (Duffy *et al.* 1987a, but see Burger & Cooper 1984). Secondly, the species is easily studied. Jackass penguins presently breed on 12 islands in the southern Benguela region (Shelton *et al.* 1984). In addition, mainland colonies have been established at Stony Point (Broni 1982, Shelton *et al.* 1984) and at Simonstown (PFIAO, unpubl. data). Jackass penguins are not only colonial, but also accessible on a regular, predictable basis at breeding sites (eg. Wilson 1985b, Duffy *et al.* 1987a). Although jackass penguins can dive to 130 m, they generally exhibit shallow diving behaviour as only approximately 2.5 % of dives exceed 20 m (Wilson & Wilson in press). They have a diurnal foraging activity and appear to feed over a relatively short period, mainly around midday (Wilson 1985c). Thirdly, penguin diet is easily sampled with the wet "off-loading" technique (Wilson 1984). However, the digestion state of prey items is highly variable (Wilson 1985c, pers. obs). This makes the analysis of life-history parameters other than length measurement - an index of age - possible only rarely. Jackass penguins breed throughout the year, but show definite breeding peaks that vary from island to island (Wilson 1985b). While at the west coast the number of breeding penguins is least during October - December (PFIAO, unpubl. data), substantial numbers of breeding penguins are found somewhere in their range at any given time of the year (Wilson 1985b). Fourthly, jackass penguins are well studied. This penguin species is endemic to the coastal region of southern Africa (Clancey 1980), and is the only member of the Order Sphenisciformes breeding on the African continent (Shelton *et al.* 1984). Largely as a consequence of the penguin population decline (Frost *et al.* 1976a, Shelton *et al.* 1984) and vulnerable conservation status (Frost *et al.* 1976a, Brooke 1984, Collar & Stuart

1985), different aspects of the species' biology have been examined. Research into jackass penguin biology has concentrated on population dynamics (eg. Jackson *et al.* 1976, Crawford & Shelton 1981, Randall & Bray 1983, Shelton *et al.* 1984, La Cock *et al.* 1987, Randall *et al.* 1987, La Cock & Cooper 1988), breeding biology (eg. Cooper 1977a, Siegfried 1977, Cooper 1980, Randall & Randall 1981, Randall 1983, Williams & Cooper 1984), physiology (eg. Erasmus & Smith 1974, Frost *et al.* 1975a, Cooper 1977b, Erasmus 1978, Erasmus *et al.* 1981, Furness & Laugksch 1983, Laugksch & Duffy 1986, Kerley & Erasmus 1987), behaviour (eg. Siegfried *et al.* 1975, Frost *et al.* 1975b, Frost *et al.* 1976b, Cooper 1977c, Eggleton & Siegfried 1979, Ryan *et al.* 1987), and particularly foraging ecology (eg. Randall *et al.* 1981, Cooper 1984, Broni 1985, Wilson 1985d, Wilson *et al.* 1985, Randall & Randall 1986, Wilson & Duffy 1986, Wilson *et al.* 1986, Wilson & Wilson (in press)).

The primary objective of this thesis was to assess the use of the jackass penguin as a sampler of the marine environment. Do penguins provide potentially useful information about marine resources such as pelagic schooling fish? Can this information aid managers of these renewable resources? I analyzed the diet of jackass penguins, samples of which were obtained from birds at colonies on the west and southwest coast of South Africa between 1980 and 1988, with respect to changes in prey composition and anchovy size-range at different time scales.

The specific aims of this thesis are three-fold:

1. to identify possible monthly and annual trends of the diet of west-coast jackass penguins in order to infer possible qualitative changes and quantify trends in aspects of pelagic fish biology
2. to identify possible differences in monthly and annual species composition and size-range of prey in penguin diet obtained from west- and southwest-coast colonies, in order to verify whether jackass penguins track populations of fish species relevant to the commercial fishery
3. to evaluate the usefulness of direct jackass penguin diet data in assessing anchovy recruitment.

In chapter one I describe the study areas and major physical, as well as biological, features of the southern Benguela. Methods of data collection and analyses are similar for all chapters and in order to avoid unnecessary repetition, these general methods are described and discussed once in chapter two. In chapter three I consider long-term diet trends of jackass penguins at the west coast of South Africa and discuss how these trends may be related to changes in the availability and abundance of prey. Chapter four presents a comparison of the diet of west- and southwest-coast penguins and considers aspects of anchovy distribution. Dietary differences are also examined in the light of differential population trends of penguins. In chapter five I apply the information on marine resources provided by penguins, and discuss the use of jackass penguins as monitors of anchovy recruitment. In the final chapter I summarize the results of my study and attempt to link the chapters into a cohesive unit.

The feeding ecology of jackass penguins has recently received considerable attention (Duffy *et al.* 1985, Wilson 1985abcd, Duffy *et al.* 1987a) and has resulted in insights into the behaviour and distribution of Cape anchovy. For example, Wilson (1985a) suggested near-shore distributed penguins feed on small schools of anchovy, rather than on large ones because distance travelled and amount of food ingested by penguins were positively correlated. Furthermore, small schools have higher surface area/volume ratios compared to large aggregations, facilitating planktivore feeding (Wilson 1985a). Thus, it may be concluded that small schools of anchovy feed inshore. Duffy *et al.* (1985) observed very small anchovy in the diet of jackass penguins on Dyer Island, and concluded that anchovy recruitment, in contrast to the traditional model of anchovy distribution (Crawford 1981a), does occur on the southwest coast of the Cape Province.

Despite the removal of factors linked to the decline of jackass penguin numbers in the first half of this century (Frost *et al.* 1976a, Rand 1971, R.J.M. Crawford pers. comm.), and the successful rehabilitation of oiled penguins (Morant *et al.* 1981), the penguin population has continued to decrease in the last three decades (Shelton *et al.* 1984, La Cock *et al.* 1987). A number of fisheries-related factors are thought to have contributed to this situation.

Jackass penguins appear to have been affected by major changes in pelagic fish populations off the southern African coast, which have occurred over the last three decades and have been attributed to overfishing by purse-seiners (Crawford & Shelton 1978, 1981; Newman & Crawford 1979, Burger & Cooper 1984). For example, pilchard was the most frequent prey in penguin diet in 1956 but was replaced by anchovy after the collapse of South African pilchard stocks (Burger & Cooper 1984). This probably resulted in a reduction of the quality of fish available to penguins, as pilchards have higher energy content and protein and fat concentrations than anchovy (Burger & Cooper 1984, Batchelor & Ross 1984). Furthermore, penguins are flightless and therefore have a limited foraging range which necessitates spatial and temporal predictability of prey (Frost *et al.* 1976a). Anchovy satisfy that requirement to a lesser degree than do pilchard (Crawford 1981a). In addition, competition between seabirds and the fishery for pelagic fishes has been suggested (eg. Crawford & Shelton 1978, 1981; Burger & Cooper 1984, Shelton *et al.* 1984). Duffy *et al.* (1987a) examined the effects of commercial fishing on the growth of chicks and diet of breeding penguins and showed that direct competition during the breeding season is limited, chiefly because breeding penguins are constrained to near-shore waters where purse-seiners cannot fish for fear of damaging their nets. Recently, low post-fledgling survival of juvenile penguins has been suggested as perhaps the most important reason for the decrease of the west-coast penguin population (La Cock *et al.* 1987, La Cock & Hänel 1987).

Chapter 1

STUDY AREAS

1.1 West coast: Jutten and Marcus Islands

During January 1987 and June 1988, field work was conducted mainly on Jutten Island (33° 05′S, 17° 57′E) but also on Marcus Island (33° 02′S, 17° 58′E). The islands lie *c.* 4 km apart at the entrance to Saldanha Bay, southwestern Cape Province, South Africa (Fig. 1.1), in the northward extension of the mediterranean climatic belt of the coastal areas of the southwestern Cape Province (Schulze 1965). Rainfall is limited to the austral winter months (May - August), the long-term annual average precipitation at nearby Cape Columbine amounting to 244 mm (Anon. 1986). Summers are warm to hot and dry (Schulze 1965), maximum temperatures reaching above 25 °C (Anon. 1986). Minimum temperatures in winter are usually above 5 °C (Anon. 1986). In summer, the wind pattern is characterized by a south-southwesterly component, forming a local derivative of the South-east Trade Winds which blow persistently during the summer months, and only intermittently during the winter months (Flemming 1977). In winter, precipitation is controlled by cyclonic northwesterly winds (Flemming 1977). The sea surface temperature range inside Saldanha Bay is 14 - 19 °C, with higher and lower temperatures occurring during summer and winter, respectively (Shannon & Stander 1977). The salinity of Saldanha Bay water shows little seasonal variation, the mean salinity of 34.9 $^{0}/_{00}$ being similar to that of the in-shore Benguela Current region (Shannon & Stander 1977).

Jutten Island is a 46 ha granite island, the third largest continental island off South Africa (Table 1, Cooper & Brooke 1986). It is sparsely vegetated except in winter (Rand 1963, pers. obs), vegetation growing among boulders scattered around the flat island perimeter and the sides of two small, *c.* 60 m high, hills (Rand 1963). The Cape cormorant is the principal breeding seabird (Cooper *et al.* 1985). Other seabirds breeding on Jutten Island are jackass penguins, crowned *P. coronatus*, bank *P. neglectus* and whitebreasted *P. carbo* cormorants, kelp *Larus dominicanus* and

Hartlaub's *L. hartlaubii* gulls and swift terns *Sterna bergii* (Brooke & Crowe 1982). Fifty-seven animal and 19 plant taxa have been recorded on the island, of which 12 and nine are alien animal and plant taxa, respectively (Cooper & Brooke 1986). Although Jutten Island supports a small population of feral European rabbits *Oryctolagus cuniculus*, which does not appear to affect breeding seabirds adversely, mammalian predators are not known to exist on the island (Cooper & Brooke 1982).

Marcus Island is a low-lying, granite 11 ha "island", joined to the mainland by a 2 km long breakwater since 1976 (Cooper *et al.* 1985). Vegetation is sparse except in winter (Rand 1963, pers. obs) and is interspersed with scattered boulders. The suite of breeding seabirds is the same as that on Jutten Island, the principal breeding seabird being the jackass penguin (Brooke & Crowe 1982). Sixty animal and 22 plant taxa have been recorded, of which nine and 12 are alien animal and plant taxa, respectively (Cooper & Brooke 1986). Feral European rabbits were present in 1960 but were extinct by December 1972 (Cooper & Brooke 1982). Fifteen species of self-introduced mammals, of which eight are potential predators of birds, were recorded on Marcus Island and the breakwater (Cooper *et al.* 1985). However, only four predators, Cape grey mongoose *Herpestes pulverulentus*, yellow mongoose *Cynictis penicillata*, small spotted genet *Genetta genetta* and Cape fox *Vulpes chama*, were recorded frequently (Cooper *et al.* 1985). The construction of a predator-proof wall in 1981 substantially reduced seabird mortalities caused by predators (Cooper *et al.* 1985).

1.2 Southwest coast: Dyer Island

Field work was conducted on Dyer Island (34° 41′S, 19° 25′E), the larger of a group of two islands situated *c.* 12 km east of Danger Point, southern Cape Province, South Africa (Fig. 1.1). Although peak precipitation occurs in the austral winter months (May – August), rainfall is not seasonally limited (Anon. 1986). Long-term annual average precipitation at Danger Point (in the first half of this century) and Cape Agulhas amounts to 546 mm and 452 mm, respectively (Anon. 1986). Maximum temperatures in summer, and minimum temperatures in winter reach above 25 °C and 12 °C, respectively (Anon. 1986). In summer, the wind pattern is characterized by southeasterly winds, generally generated by the South Atlantic high-pressure system (Boyd *et al.* 1985). Variable westerlies occur during winter, northwesterly winds dominating (Boyd *et al.* 1985). Winter winds are associated with east-moving cyclonic low-pressure systems impinging on the southern tip of Africa (Boyd *et al.* 1985). Averaged and smoothed sea-surface temperatures derived from satellite imagery for November - January, February - April and May - October are 18 - 19 °C, 17 - 18 °C and 15 - 16 °C, respectively (Fig. 6, Kamstra 1985).

Dyer Island is an elongated, low-lying island about 7 m above sea level (Rand 1963, pers. obs), and 20 ha in size (Cooper & Brooke 1986). The surface is flat and pebble-covered, topped with mixed vegetation (Rand 1963). The jackass penguin and Cape cormorant are the principal breeding seabirds (Cooper *et al.* 1985). Other breeding seabirds are crowned, bank and whitebreasted cormorants, kelp, Hartlaub's and greyheaded *L. cirrocephalus* gulls, swift and Caspian *S. caspia* terns (Brooke & Crowe 1982). Sixty-one animal and 14 plant taxa have been recorded on the island, of which 10 and six are alien animal and plant taxa, respectively (Cooper & Brooke 1986). Apart from the musk *Suncus murinus* and lesser dwarf *S. varilla* shrews, recorded on the island in 1912/3 and 1981, respectively, no other mammals are known to have been introduced to Dyer Island (Cooper *et al.* 1985). Hauled-out Cape fur seals *Arctocephalus pusillus*, presumably from nearby Geyser Island, have been observed at the southwestern part of the island (pers. obs). For a complete description of faunistic and floristic surveys see Brooke & Crowe (1982) and Brooke & Prins (1986).

1.3 Southern Benguela system

The foraging area of jackass penguins at both west and southwest coast study areas is located within the southern Benguela system, the area off the southwest coast of the Cape Province south of 32° S (Fig. 1.2). The Benguela is one of the four major eastern boundary current regions of the world, characterized by equatorward surface flow, coastal upwelling, similar ichthyofaunal assemblages (Parrish *et al.* 1983), and high biological productivity (Cushing 1971a).

The bathymetry of the southern Benguela changes from a continental shelf of varying width between 32° and 34° S, to the broad and shallow Agulhas Bank (centred at 35° S and 21° E) at the southernmost margin of the continent (Shannon 1985) (Fig. 1.2). The Agulhas Bank separates the warm Agulhas Current in the east from the cool Benguela upwelling system in the west (Boyd *et al.* 1985). Nelson & Hutchings (1983) regard the contribution of Agulhas water to the flow over the west coast shelf as small but continuous. South of the Agulhas Bank, the Agulhas Current executes a retroflection, forming shear-edge eddies and rings (Shannon 1985).

Upwelling is a wind-induced process, whereby off-shore Ekman transport of surface water results in upwelling of cold, nutrient-rich water. Upwelling in the southern Benguela varies spatially and temporally. The width of the coastal upwelling regime may be 150-200 km on average, although the filamentous mixing area, consisting of upwelling plumes, streamers, eddies and filaments seaward of the main upwelling front, may extend 625 km offshore (Lutjeharms & Stockton 1987). Upwelling is most prevalent from September/October to March (Andrews & Hutchings 1980, Shannon & Pillar 1986).

Important upwelling centres are Cape Columbine and the Cape Peninsula (Shannon 1985). While upwelling extends as far eastwards as Cape Agulhas (Shannon 1985), it is less intense and frequent in the Danger Point area than off the Cape Peninsula, because of more relaxed atmospheric forcing (Jury 1988). Upwelling has also been shown to occur over the Agulhas Bank from satellite imagery (Harris 1978, Walker 1986, Lutjeharms & Stockton 1987).

The dynamics of the southern Benguela upwelling system are mainly controlled by mesoscale atmospheric perturbations, bathymetry and topography, and the influence of the Agulhas Current system (Shannon 1985). Prevailing winds in the southern Benguela are determined by the South Atlantic high pressure cell (anticyclone), eastward moving cyclones, and the pressure field over southern Africa (Nelson & Hutchings 1983, Shannon 1985). Wind relaxation or reversals associated with easterly moving cyclones not impinging on the southern African continent, give rise to pulsed upwelling with a period of about three to six days (Nelson & Hutchings 1983, Shannon 1985). As a result of the narrow continental shelf off Cape Columbine and the Cape Peninsula, cold water is available at subsurface depths close inshore (Shannon 1985), facilitating upwelling.

During active upwelling cold, nutrient-enriched water reaches the surface near the shore (Chapman & Shannon 1985), enhancing primary productivity and resulting in a less diverse phytoplankton species composition than in warm, stable water (Brown & Hutchings 1985). Sea surface temperatures of newly upwelled water may be less than 9 °C (Shannon *et al.* 1981, cited by Shannon *et al.* 1985). Phytoplankton, generally dominated by chain-forming diatoms, colonize the upwelled waters (Brown & Hutchings 1985, Brown & Hutchings 1987a), depleting nutrients in the upper layers after the establishment of the thermocline (Chapman & Shannon 1985). Consequently, phytoplankton blooms grow and decline. Brown & Hutchings (1987a) estimate the period of growth and decline to be three and 3 – 4 days, respectively. Nitrates, and sometimes silicates, appear to limit phytoplankton production (Chapman & Shannon 1985, Brown & Hutchings 1987b). From satellite imagery, highest near-surface chlorophyll concentrations during sustained upwelling were observed downstream from main upwelling centres (Shannon *et al.* 1985). Phytoplankton biomass is higher and more variable in summer than in winter (Shannon & Pillar 1986). Whereas in winter chlorophyll-*a* concentrations integrated over the upper 50 m are low to moderate and uniformly distributed over the entire coastal zone, frequent upwelling events in summer concentrate chlorophyll-rich waters in a narrow band along the coast as far as Cape Agulhas (Shannon *et al.* 1984a). On the Agulhas Bank moderate and widespread chlorophyll concentrations are observed in autumn and spring, mixing and stratification of the water column imposing this seasonal cycle (Shannon *et al.* 1984a). In late summer and autumn, a subsurface chlorophyll maximum is associated with the thermocline (Shannon *et al.* 1984a, Carter *et al.* 1987).

After phytoplankton production, zooplankton growth occurs in upwelling cells (Hutchings & Nelson 1985). The biomass of euphausiids and copepods is higher at the west coast than at the Agulhas Bank area, copepods constituting 90 and 68 % of total biomass in each area, respectively (Pillar 1986). Biomass variability is highest inshore (Pillar 1986).

Bergh *et al.* (1985) have calculated that 75 % of the phytoplankton becomes detritus. High standing stocks or mean phytoplankton concentrations are therefore not necessarily relevant in trophic interactions in terms of food supply to higher levels (Brown & Hutchings 1985), as zooplankton and fish may be unable to respond to patchy phytoplankton blooms fast enough to utilize them fully (Bergh *et al.* 1985).

Coastal upwelling of nutrient-rich water and concomitant high primary production create a suitable habitat for pelagic schooling fish (Cushing 1971a), which form the basis of an important commercial fisheries in the Benguela system. The development of the fisheries has been described by De Villiers (1985) and the major fish and invertebrate resources of the Benguela ecosystem have been reviewed by Crawford *et al.* (1987). The purse-seine fishery off South Africa has been based largely on Cape anchovy *Engraulis capensis* [= *E. japonicus*], South African pilchard *Sardinops ocellatus* [= *S. ocellata*], Cape horse mackerel or maasbanker *Trachurus trachurus* and southern African round herring or red-eye *Etrumeus whiteheadii* [= *E. teres* = *E. micropus*] (Crawford *et al.* 1987).

Cape anchovy in the southern Benguela region exhibit an annual seasonal migration pattern, first inferred from commercial catch data (Crawford 1980, 1981a) and subsequently confirmed by direct hydroacoustic surveys (Hampton 1987). The current model of anchovy distribution during normal years holds that anchovy spawn toward the edge of the Agulhas Bank on the south coast of South Africa between October and February (Crawford *et al.* 1987). Eggs and larvae are subsequently transported by a frontal "jet current" northwards to the nursery area in the St Helena region at the west coast, or farther north (Shelton & Hutchings 1982). During the austral autumn/winter, the recruits migrate southward along the west coast to reach the spawning grounds in the austral spring/summer. During this southward migration these 0-year-old fish are concentrated close inshore (Hampton 1987). Older, i.e. one- and two-year-old, fish are generally found east of Cape Agulhas (Hampton 1987).

Distinct seasonal cycles characterize the spawning, recruitment, distribution and movements of fish species in the southern Benguela (Crawford 1980, Crawford *et al.* 1987). Anchovy and pilchard are spring/summer spawners and similarities in aspects of their distributional ecology have been noted (Crawford *et al.* 1987). With the advent of spring, young fish migrate southerly to warmer waters east of Cape Point where spawning of anchovy and pilchard occurs between October – February (Crawford 1981a) and September – February (Crawford 1981b), respectively. Anchovy are not as long-lived as pilchard and spawn in similar regions to those of the younger pilchard adults (Crawford *et al.* 1987). Juveniles of the two species recruit to the west coast purse-seine fishery in autumn/winter. Anchovy recruits become available to the fisheries between February and September, with a maximum in June (Crawford 1980). In autumn one-year-old anchovy migrate to the east, similar to the movement of two- and four-year-old pilchard (Crawford 1980).

In contrast to anchovy and pilchard, the distributional ecology of maasbanker (Crawford 1981c) and red-eye (Crawford 1981d) is less well-known. Spawning of maasbanker and red-eye occurs throughout the year, but is maximal in winter/spring (Crawford 1981c, Shelton 1986). Maasbanker eggs and larvae occur west of Cape Columbine, at the western edge of the Agulhas Bank (Crawford *et al.* 1987) and in deep water offshore (Crawford 1980, Shannon & Pillar 1986). Spawning of red-eye occurs mainly between Cape Columbine and Cape Point near the 200 m isobath and is maximal from August to October (Shelton 1986, Crawford *et al.* 1987). Recruitment of nought-year-old maasbanker takes place during May and June in the St Helena region (Crawford 1980). Young red-eye move south- and eastwards at the conclusion of winter and recruit along South Africa's west coast between April and September (Crawford *et al.* 1987). Juveniles of all four species frequently occur together in mixed shoals (Crawford 1980). The main predators of these fish species include the Cape fur seal, jackass penguin, Cape gannet and Cape cormorant, as well as various tuna species (Crawford 1980).

The ecology of seabirds in the Benguela ecosystem has been reviewed by Berruti *et al.* (1989). The marine avifauna in that region comprises 12 breeding seabirds of which nine are endemic taxa, and 36 species which are regular non-breeding visitors (Berruti *et al.* 1989).

and annual frequency of occurrence of prey items were analyzed in order to determine possible changes in prey availability. A generalized linear model was fitted to frequency of occurrence data, using a logarithmic link function and binomial error distribution appropriate for data in the form of proportions (McCullagh & Nelder 1983).

2.1.2 Frequency of abundance

Absolute and relative frequency of abundance were used in the numerical analysis of prey items. Absolute frequency of abundance is the number of items of a particular prey type per stomach (Duffy & Jackson 1986). Relative frequency of abundance is the proportion of one particular prey type out of all prey types (Duffy & Jackson 1986), and is therefore relative to other prey types present in the stomach sample. The diet of jackass penguins consists mainly of pelagic schooling prey (Wilson 1985a, Duffy *et al.* 1987a). Since penguins presumably maximize foraging efficiency and therefore feed on as many fish as possible from one encounter with a particular school of pelagic fish, the selection of prey types may not be independent. The assumption of random sampling (of individual prey items) is thus not valid and, consequently, absolute and relative frequency of abundance of prey items cannot be analyzed statistically. However, in order to determine possible seasonal trends in the composition of jackass penguin prey species, monthly absolute frequencies of abundance of jackass penguin prey items were analyzed graphically using simple correspondence analysis (program CA of BMDP88). Monthly absolute frequency of abundance was derived by summing the number of items of a particular prey type per stomach in each month.

Correspondence analysis (Benezécri 1973, cited by Greenacre 1984) is a multivariate technique equivalent in theory to reciprocal averaging (Hill 1974, Orlóci 1978) and dual (or optimal) scaling (Nishisato 1980). It is one of a family of graphical display techniques that involve the calculation of the singular value decomposition of a data matrix (eg. principal component analysis, biplot, canonical correlation analysis, discriminant analysis, factor analysis) (Greenacre & Underhill 1982, Underhill & Peisach 1985). For a detailed discussion of the theory and applications of correspondence analysis see Greenacre (1984).

Correspondence analysis is primarily a geometric technique which reduces the dimensionality of a set, or "cloud", of points in multidimensional space (Greenacre 1984). The frequency of absolute abundance data of different prey species in different months in west-coast jackass penguin diet is a matrix consisting of rows (or objects, i.e. months) and columns (or variables, i.e. prey species). The row and column profiles (i.e. relative frequencies of row and column data) may be thought of as one joint cloud of points in multi-dimensional space. The graphical display of correspondence analysis is the subspace of lower dimensionality which represents as accurately as possible the points' true high-dimensional positions (Greenacre & Vrba 1984). The geometry of each cloud of variable and object profiles is directly related (Greenacre 1984). Hence the analysis displays both the rows and columns simultaneously. In the graphical display of each cloud of points, the distance between points indicates the degree of similarity between object or variable profiles, similar ones being close together and dissimilar ones farther apart (Greenacre 1984). The joint interpretation of object and variable points occurs through so-called "transition formulae" (Greenacre 1984, Underhill & Peisach 1985): a particular row profile tends to a position which corresponds to the column categories which are prominent in that row profile (Greenacre 1984). Furthermore, variables situated close to the origin are most typical of the greatest number of objects, i.e. prey species close to the origin tend to occur in similar proportions in most months. Objects or variables which differ markedly from the rest of the data, or swamp the data, tend to dominate the analysis. Their effect is neutralized by excluding them from the analysis but including them in the graphical display as supplementary points (Greenacre 1984, Underhill & Peisach 1985). This allows the analysis of more subtle multivariate relationships within the remaining data.

Graphical displays produced by the correspondence analysis are supplemented by a series of tables which determine the distortion of the two-dimensional representation of the row and object points' true high-dimensional positions. The most important tables for the interpretation of the display are those detailing the decomposition of the total inertia for the objects and variables. Total inertia is the sum of the squared singular values (or eigenvalues), and is a measure of how much the individual profiles are spread

2.2.1 Size-frequency distribution

Anchovy size-frequency distributions were compared statistically and by inspection, in order to determine possible trends of anchovy length within and between years and localities. For testing whether two samples have been drawn from populations with the same distribution, the Kolmogorov-Smirnov two-sample test (Siegel 1956) appears to be more appropriate than Conover's (1971) chi-square test for differences in probabilities. However, in contrast to the chi-square test, it is not applicable to multisample testing - a requirement of monthly and annual size-frequency distribution analyses. The chi-square test for differences in probabilities, employing the T test statistic, was consequently used. This test was invalid if a contingency table had an expected frequency of < 1 in any cell and/or expected frequencies < 5 in more than 20 % of its cells (Cochran 1954; cited by Conover 1971, Zar 1984).

Size-frequency distributions of Cape anchovy obtained from west- and southwest-coast jackass penguin diet samples were separately analyzed statistically. Monthly size (i.e. length) frequency distributions of 5 mm class intervals were compiled from all the available anchovy caudal length data from all stomach samples in one month. In order not to invalidate the chi-square analysis of contingency tables, the intervals of the lower and upper length intervals of size-frequency distributions were combined into < 56 and > 90 mm length intervals, respectively. Contracted length distributions were thus comprised of nine (or fewer) 5 mm size intervals.

Monthly size-frequency distributions of the same month in different years were tested for heterogeneity by testing for an overall significant difference. Annual length distributions were derived by summing all the available fish length data within years. Annual length compositions of different years were tested for heterogeneity by testing for an overall significant difference.

2.2.2 Median length

Although size-frequency distributions allow identification of trends in change of monthly and annual anchovy lengths by inspection, length frequency distributions cannot be used in quantifying those trends. For that purpose an analysis of interval data is required, and a summary, describing an important property of all monthly and annual fish lengths, is useful. Measures of central tendency indicate "where, among all the possible values of a variable, the sample or population is located" (Zar 1984, pg. 18), and thus represent such a summary. The median was used as a measure of central tendency of anchovy caudal lengths, as the mean is affected by extreme values (Zar 1984), extreme anchovy lengths occurring in many months (pers. obs). Nonparametric two- and multisample median tests which utilize chi-square analysis of contingency tables (χ^2 statistic) (Mood 1950) were used to establish and analyze trends in median lengths. The Yates correction for continuity was not applied in the two-sample median tests (Zar 1984), as sample sizes were large (pers. obs).

The normal approximation to the Mann-Whitney test (with tied ranks), and the Kruskal-Wallis test (with correction factor for tied ranks) for nonparametric ANOVA (Zar 1984), are further procedures for the respective analysis of two- and multisample interval data. They are different from the previous two tests, in that their underlying null-hypothesis makes no statement about the location of the population or sample among all the possible values of a variable. Although ranks must be assigned to anchovy length measurements in all four tests (two- and multisample median tests, Mann-Whitney and Kruskal-Wallis tests), tied ranks need only be computed in the latter two. This, and the fact that the sum of actual ranks are used in the computation of the test statistic, renders the Mann-Whitney and Kruskal-Wallis tests unsuitable for the large anchovy length data set analyzed here. The two- and multisample median tests employ the rank of a measurement itself in the calculation of the test statistic which is therefore less tedious to compute. Consequently, the use of median tests in the analysis of possible trends in monthly and annual anchovy lengths is justified.

Median anchovy lengths obtained from west- and southwest-coast jackass penguin diet samples were analyzed separately. For monthly anchovy median length determinations all the available caudal length data from all stomach samples in one month were combined. Relevant size-frequency distributions, established in 2.2.1 above, were used to calculate medians. A method appropriate for the median within a size interval containing tied observations was employed. That is,

median = (lower limit of interval) +
((0.5 x sample size - cum. freq.) /
(no. of observations in interval)) x
(interval size),

where "cum. freq." is the cumulative frequency of the previous classes (Zar 1984). Annual median lengths were determined by combining all the available caudal length data from all stomach samples within years. Possible overall significant differences in annual anchovy median lengths and monthly median lengths of the same month in different years were detected using the multisample median test (Mood 1950). If overall significant differences between annual median lengths were established, years between which significant differences existed, were identified. A Tukey-type multiple comparison test is available for that purpose (Levy 1979, cited by Zar 1984), but requires equal sample sizes (Zar 1984). Although a harmonic mean sample size for "slightly unequal" sample sizes can be employed (Zar 1984), monthly anchovy caudal length sample sizes differed greatly (pers. obs) and could not be considered "slightly unequal". In multisample analyses, therefore, non-overlapping of ≥ 95 % confidence intervals was taken as indicating significant differences at approximately the 0.05 level (McGill *et al.* 1978). The ≥ 95 % confidence interval around median lengths was determined. A large-sample approximation of the lower confidence limit was used (Zar 1984).

2.3 Sample size evaluation

Morrison (1986, pg. 276) called for an evaluation and justification of the sample size of data analyzed since without this, one does not know "if the results are due to the biology of the animals or the inadequacy of the samples". At the west coast, Duffy *et al.* (1987a) obtained a minimum of 10 diet samples per growth period, generally resulting in the collection of at least 20 samples per month. A minimum of 20 jackass penguin stomach samples per month was subsequently collected at the west coast, and throughout the monitoring of southwest-coast penguin diet. Between July 1980 and June 1988, the mean (± 1 SD) number of monthly diet samples collected at both localities was 19.9 (± 8.6), after outliers were identified and removed. No significant difference existed between the mean number of monthly samples collected at the west (19.4 ± 8.9) and southwest (21.3 ± 7.5) coasts (df = 71, $t = -0.8120$, P > > 0.05).

The adequacy of prey composition data is difficult to establish. Assuming prey distribution is not anomalous, variation in the frequency of occurrence of particular prey species in a jackass penguin stomach sample at a given locality and time should decrease and stabilize at increasing sample sizes. Furthermore, an increase in the occurrence of "rare" prey species can be expected. Further analyses are needed to determine whether the variation in the probability of prey occurrence, based on 19.9 samples per month, is acceptable. Frequency of absolute abundance will increase with increasing sample size, although an upper limit is expected for any given prey size since the volume of any stomach is limited.

Only for median anchovy lengths was an evaluation of stomach sample size for anchovy size-range completed. The relative contributions of length intervals to anchovy size-frequency distributions at a given locality and month were assumed to stabilize with increasing sample size. This assumption was not tested.

For median anchovy lengths, the size of the ≥ 95 % confidence interval range is an indication of the reliability of the sample size. Since the median is concerned with the rank of a measurement and not the value of the actual measurement itself, the number of fish used in the median calculation, and the distribution of the fish lengths between the length intervals, will determine the width of the confidence interval range. Only the confidence interval range is considered here.

Exponential regression of ≥ 95 % confidence interval range of median anchovy length on the number of fish measured (Fig. 2.1) was highly significant (df = 1,7; $F = 48.23$, $P < 0.00001$, $r^2 = 0.405$)

$$\text{CI range} = e^{2.26 - 0.0034\,(\text{no. of fish})}. \tag{2.1}$$

Standard error of the slope is 4.9×10^{-4}. Simple linear regression of the number of fish measured on the number of jackass penguin stomach samples obtained (Fig. 2.2) was also significant (df = 1,7; $F = 15.95$, $P < 0.0005$, $r^2 = 0.183$)

$$\text{no. of fish} = 64.9 + 6.9\ (\text{no. of stomach samples}). \qquad (2.2)$$

The standard error of the slope is 1.7 fish per stomach sample. No significant difference (df = 71, $t = -1.240$, $P > 0.05$) in the mean monthly number of anchovy measured from west- and southwest-coast jackass penguin diet samples was detected. Combining jackass penguin diet data from both locations, the mean (± 1 SD) number of anchovy measured per month was 202 (± 137). Month and number of fish measured monthly were not significantly correlated ($n = 73$, $r = 0.2014$, $P > 0.05$). Although confidence interval range was significantly correlated to number of stomach samples ($n = 73$, $r = -0.2467$, $P < 0.05$), a larger amount of variation in confidence interval range was explained by consecutive application of the above two regressions. Hence, the number of stomach samples required for a chosen level of precision can be calculated using equations 2.1 and 2.2. For the west and southwest coasts and pooled jackass penguin diet data, the ≥ 95 % confidence interval range of anchovy median length was approximately 5 mm. The confidence interval range increased to about 6 mm when one SD was subtracted from the number of stomach samples obtained. This means that for 66.7 % of jackass penguin stomach samples obtained, the ≥ 95 % confidence interval range of anchovy median length was 6 mm. The accuracy of the original equation relating anchovy otolith length to fish length is unknown but it seems unlikely that it was greater than 3 mm.

Although the monthly sample size analysis of west- and southwest-coast jackass penguin diet presented here is a *posteriori* one, it nevertheless justifies the number of stomach samples collected and thus evaluates the reliability of the information obtained.

Chapter 3

LONG-TERM DIET TRENDS OF JACKASS PENGUINS ON THE WEST COAST OF SOUTH AFRICA

3.1 Introduction

Studies of the foraging ecology of seabirds may elucidate not only the biology of the bird species concerned but may also allow inferences to be made about specific parameters of the biology of their prey. Thus seabird diet may potentially provide information useful in the management of commercial fisheries (eg. Berruti 1987). Recently attention has been given to jackass penguin diet as a means of assessing the marine environment (eg. Duffy *et al.* 1985, Wilson 1985a).

The first investigations of the diet of jackass penguins commenced in the 1950s and were prompted by concern for the potential impact of penguins on commercial fish stocks in the Benguela region (Davies 1955, 1956, 1958; Rand 1960). Since the late 1970s, the feeding ecology of the jackass penguin has once again received considerable attention (Duffy *et al.* 1985, Wilson 1985abc, Duffy *et al.* 1987a, Laugksch *et al.* 1988), largely to evaluate the perceived effects of the commercial fishery on the penguin population. Comparisons of diet changes between decades (eg. Crawford & Shelton 1981, Burger & Cooper 1984, Cooper 1984) were based primarily on "one off" studies, although Duffy *et al.* (1987a) compared fishery landings with the growth and diet of penguins between 1980 and 1985.

In this chapter, an extended nine-year time series of the diet of west-coast jackass penguins between 1980 and 1988 is analyzed for the presence or absence of qualitative changes or quantified trends in the biology of five of their most important prey species: anchovy, pilchard, maasbanker, red-eye and cephalopods. With the exception of cephalopods, the above prey species are important to the South African purse-seine fishery, particularly anchovy (Crawford *et al.* 1987).

Results are interpreted in the light of the jackass penguin as a possible qualitative or quantitative sampler of the pelagic fish of the southern Benguela region. As no base line data with respect to abundance and size of prey exist for prey other than anchovy (eg. Hampton 1987), comparisons of penguin diet-based data with commercial fishery catch-based data were made to verify any possible trends found.

3.2 Methods

General methods of data collection and analyses of frequency of occurrence and abundance of prey species (prey composition) and anchovy size-frequency distributions and median lengths (anchovy size-range) are described in chapter two. Details of further procedures relevant to this chapter are described below.

3.2.1 Prey composition

PENGUINS

The number of jackass penguin stomach samples obtained annually between July/August and January was usually small. Consequently, in order to overcome possible seasonal bias in annual prey composition and anchovy size-range, annual data for 1983-1987 and 1981/88 were obtained by only summing available monthly data from February to August, and February to June, respectively.

<u>Frequency of abundance</u>

Mass (and/or volume) is clearly the preferred method of estimating abundance of prey items in seabird diet (Duffy & Jackson 1986). However, due to the highly variable state of digestion of prey items recovered from penguin stomach samples (pers. obs), the mass of intact pelagic fish could only be back-calculated from otolith length. Such otolith data for species other than anchovy are not available for the early years of this nine-year data series, and comparisons with these years are therefore not possible.

Because of the small sample size of diet samples collected in 1982, annual data for 1982 were excluded (cf. chapter two). Only from 1982 onwards were red-eye listed in jackass penguin diet. In order to analyze maximum possible multivariate relationships within jackass penguin prey species, the correspondence analysis of monthly prey species composition was performed on 1983-88 data only.

distributions of anchovy in commercial landings between January and June each year during 1985–88 were calculated. This corresponds to the interval for which a large number of penguin diet samples are available (cf. Table 3.1). The maximum theoretical foraging range of breeding jackass penguins is 24.2 km (Wilson 1985a). Penguins have a near-shore distribution at sea and travel north and south from the entrance to Saldanha Bay (Wilson 1985a). South African purse-seine fishery pool areas seven and eight overlap the penguins' largest possible foraging range along the coast (Fig. 3.1). Anchovy caudal length data for these two areas, obtained from the Sea Fisheries Research Institute (unpubl. data), were summed. For months in which no anchovy landings were made in pool areas seven and eight, data from area six (Fig. 3.1) were used.

Median lengths

To investigate whether diet-based trends in anchovy lengths were indicative of general trends of the total anchovy population, monthly length distributions of total anchovy landings (South African purse-seine fishery pool areas one to 20) between February and August in 1983–88 were pooled. The annual median lengths were calculated and compared with those of anchovy taken by west-coast jackass penguins.

3.3 Results

At Marcus and Jutten Islands, 1 157 jackass penguin stomach samples were collected during 59 months, between July 1980 and June 1988 (Table 3.1). Each month was not equally sampled, more samples being collected in the first half of the year than in the second (Table 3.1).

3.3.1 Prey composition

Frequency of occurrence

Monthly and annual probability of occurrence of anchovy, pilchard, maasbanker, red-eye and cephalopods in the diet of west-coast jackass penguins were derived from a generalized linear model. The model took into account differences in sample size, and thus probabilities of occurrence are comparable (cf. Table 3.1).

Monthly trends

In contrast to the monthly probability of occurrence of pilchard, maasbanker, red-eye and cephalopods, that of anchovy was high throughout the year, reaching above 0.8 in all months except November (Fig. 3.2). Although individual monthly probabilities of the other four pelagic prey species varied, they generally showed an inverse trend throughout the year to that exhibited by anchovy (Fig. 3.3). Probability of occurrence of maasbanker, red-eye and cephalopods increased after reaching a low in July - August and May, respectively. Only pilchard continued to decrease after the mid-year low and increasing again only in November (Fig. 3.3). In November, cephalopods were equally likely as anchovy to occur in penguin diet (Fig. 3.3).

Annual trends

Annual probability of occurrence of anchovy during 1980 - 1988 increased in 1981 after a low in 1980. Probability of occurrence remained above 0.9 between 1983-84 and subsequently decreased to 1986 (Fig. 3.4). Thereafter, the probability increased to 0.99 in 1988. The trends in annual probability of occurrence of pilchard, maasbanker, red-eye and cephalopods were generally low and differed from that of anchovy (Fig. 3.4 - 3.5). Probability of occurrence of pilchard was comparatively high in 1987 (Fig. 3.5).

Frequency of abundance

A total of 19 027 prey items was obtained from west-coast jackass penguin stomach samples during 1980 - 1988. Anchovy constituted 68.2 % of all prey items obtained, and together with maasbanker, red-eye, pilchard and cephalopods accounted for 78.1 % of all prey items found in penguin stomach contents (Table 3.2). Annual relative frequencies of numerical abundance of the above species in the diet of jackass penguin are presented in Table 3.3. Relative anchovy abundance was low in 1982, and high in

The decomposition of the total inertia of years of the correspondence analysis of the prey species composition of annual diet- and catch-based abundance data are presented in Tables 3.5 - 3.6, respectively. The identical sign of the coordinates of years and prey species on the relevant axis indicates that in west-coast penguin diet, the years 1987, 1984/85 and 1983/86 (Table 3.5) were associated with high proportions of pilchard, maasbanker and red-eye (Table 3.7), respectively. These trends were also evident from the graphical display of the two principal dimensions of the analysis (Fig. 3.7). Only two trends in penguin diet were also reflected by the purse-seine fishery CPUE data. Firstly, the association between 1987 and pilchard was evident in the catch-based display (Fig. 3.8), although that year was associated with maasbanker as well (Tables 3.6 and 3.8). Secondly, both 1983 and 1986 appeared to be associated with red-eye in the catch-based display (Fig. 3.8). This is a misinterpretation, as 1983 was in fact marginally associated with pilchard, but not with red-eye (Tables 3.6 and 3.8).

3.3.2 Anchovy size-range

Between July 1980 and June 1988, 12 649 anchovy recovered from jackass penguins were measured. The small sample size in 1982 and January 1986 precluded analysis.

<u>Size-frequency distributions</u>

Monthly trends

There was considerable monthly variation in the length of anchovy taken by penguins on the west coast (Figs 3.9 - 3.11). The range in anchovy length was greatest in the first half of each year, mainly between March and June/July, and was due to an influx of small fish (Figs 3.9 - 3.11). After July, small anchovy usually no longer appeared in penguin diet and the range in anchovy length decreased. This decrease was not necessarily accompanied by a shift to larger anchovy. Compared with pre-1984 years, penguins appeared to take a much smaller proportion of large anchovy (> 100 mm in caudal length) after 1984 (Figs 3.9 - 3.11).

Inter-annual monthly size-frequency distributions of anchovy in penguin diet were heterogeneous in all months (Table 3.9). Thus monthly anchovy length data of the same month in different years could not be justifiably pooled, precluding statistical analyses of inter-annual monthly trends.

Except in January 1987, anchovy in both fishery landings and west-coast jackass penguin diet were larger in the first part of the year in 1987-8 than in 1985-6 (Fig. 3.12). From May to July, differences in anchovy length distributions between 1985-6 and 1987-8 were less pronounced. No anchovy catches were recorded in purse-seine fishery pool areas six, seven and eight in January - March 1986.

Annual trends

The July - August 1980 size-frequency distribution was not significantly different from the February - June 1981 distribution (df = 8, χ^2 = 11.91, P > 0.05). Consequently, 1980 was included in the analysis of anchovy length data. There was a significant overall difference in the annual size-frequency distributions of anchovy taken by west-coast jackass penguins during the eight-year period between 1980-88, excluding 1982 (df = 56, χ^2 = 2811, P < 0.0001). Size distributions showed a clear shift in emphasis from large (> 90 mm) to small (< 56 mm) fish between 1980 and 1988 (Fig. 3.13). The changes in the proportion of large and small fish in penguin diet appeared to have taken place between 1981 and 1983, and between 1984 and 1985.

Median lengths

Monthly trends

Trends in monthly median lengths were similar to those obtained from size-frequency distributions. Intra-annual median lengths were not further analyzed. In most years minimum median length occurred in March or April. In 1985-88 a second dip in median length occurred in July (Fig. 3.14).

Pooling of inter-annual monthly median lengths was not justified, as overall significant differences occurred in January to September (Table 3.9). Statistical analyses of these median lengths were therefore not possible.

Monthly trends

Frequency and probability are here used as interchangeable terms, although the latter carries a predictive connotation. Duffy & Jackson (1986) regard frequency of occurrence as a measure of prey abundance. However, it is clear that frequency of occurrence is primarily a measure of prey availability (Wiens 1984) (cf. Fig. 3.16).

The monthly probability of occurrence of anchovy in jackass penguin diet was lower in months in the first, than in the second part of the year (Fig. 3.2) and trends therefore appear to be inconsistent with the anchovy migration pattern. Recruits undergo a seasonal southward migration along the west coast early in the year (Crawford 1980, 1981a, Hampton 1987). The migration results in the concentration of anchovy recruits close inshore (Hampton 1987), and as jackass penguins are flightless and thus have a limited foraging range (Frost *et al.* 1976a), the availability of anchovy recruits to penguins is expected to increase during the migration. However, since timing of the annual migration pattern is variable (see below and chapter five), it is unlikely that detailed trends are reflected in monthly probabilities of occurrence averaged over the period 1980–88.

Availability of anchovy was highest during July/August, approximately the same time as the availability of anchovy recruits to the fishery is considered to be at a maximum (Crawford 1980, 1981a). Furthermore, anchovy were least likely to occur in penguin diet during November (Fig. 3.2). As anchovy move eastwards and offshore over the Agulhas Bank with increasing age (Hampton 1987), and spawned eggs and larvae are only beginning to develop, the decreased availability of anchovy at the west coast after the beginning of the spawning season in October (Hampton 1987) is expected.

The trend in the variation of intra-annual monthly anchovy lengths in the diet of foraging jackass penguins on the west coast reflected the annual migration pattern of anchovy much clearer than frequency of occurrence. Data from shorter time series than the one analyzed here (Wilson 1985b, Duffy *et al.* 1987a) already indicated that small anchovy appeared to be predominant in the diet of west-coast jackass penguins in the first part of the year. In this long-term data series, a consistent shift to smaller length classes was demonstrated in the first part of years 1981-88. This indicated a distinct seasonal, annual wave of small anchovy between March and June/July. Quantitative aspects and possible implications of this trend for the South African anchovy fishery are discussed in chapter five.

Shelton *et al.* (1988) showed that during the summer of 1986-7 and 1987-8 the distribution of anchovy was unusual. Spawner biomass and egg production surveys revealed a high abundance of adult fish and eggs on the west coast in November 1986 and 1987, in contrast to surveys conducted in 1983 - 1985 (Shelton *et al.* 1988). The shift to larger anchovy caught by the commercial fishery between 1985-6 and 1987-8 was attributed to the good availability of adults on the west coast (Shelton *et al.* 1988). Over the same period, length distributions of anchovy in penguin diet exhibited a similar trend, i.e. anchovy in the first part of the year in the latter period were larger than in the former (Fig. 3.12). This indicated that this anomalous anchovy distribution was reflected in penguin diet.

Whereas the analysis of the nine-year data series of 1980-88 indicated that the monthly probability of occurrence of anchovy was lowest in the period after October (Fig. 3.2), Wilson (1985b) showed that during July 1980 and June 1981 the frequency of occurrence of anchovy in the diet of jackass penguins at Marcus Island was lowest between February - March. This suggested that an annual pattern of availability of anchovy to west-coast jackass penguin exists, but that the timing of anchovy migration, and thus spawning, is variable.

The heterogeneity of inter-annual monthly size-frequency distributions and median lengths of anchovy taken by jackass penguins further indicated that the annual occurrence of the influx of small anchovy varies from year to year. This is expected, as survival and growth in the embryonic, larval and juvenile stages of anchovy are affected by intra-population and environmental factors (Smith 1985) which, in the unstable and unpredictable southern Benguela (Shannon 1985), cannot be regarded as constant between years.

At short (Fig. 1, Wilson 1985b) and at long time intervals (this study), a drop in the probability of occurrence (and hence availability) of anchovy coincided with an increase in that of prey species other than anchovy (Figs 3.2 - 3.3). Frequency of abundance is regarded as a measure of the frequency of prey encounter (Duffy & Jackson 1986), however Berruti (1987) suggested that frequency of occurrence was more appropriate for shoaling species. Using this latter measure, the inverse trend of the frequency of occurrence of anchovy and other penguin prey species could be accounted for. If it is assumed that during periods of low anchovy availability, penguins are required to forage on species other than anchovy as well, a higher frequency of prey encounter with other prey species occurs in such periods. The trends of occurrence of the other fish species are therefore dependent on the trend of anchovy. Thus only the trend in anchovy occurrence, and hence availability, was justifiably interpreted in the light of pelagic schooling fish distribution and migration patterns.

The composition of prey species (other than anchovy) taken by jackass penguins at the west coast did not vary seasonally (Fig. 3.6). The dependence of penguins on anchovy suggested that, within the penguins' foraging range, other pelagic shoaling fish were either available in small, scattered shoals, or relatively unavailable to penguins (but see Wilson 1985a).

Annual trends

Frequency of occurrence

Analyses of sea-surface temperatures (SST) of the Southeast Atlantic showed that positive SST anomalies had occurred in that region since 1983 (Shannon & Agenbag 1987, Taunton-Clark & Shannon 1988). In a recent study of the responses of fish populations in the Benguela ecosystem to environmental change, Shannon *et al.* (1988) found that warm periods generally favoured epipelagic fish. They thus attributed the good recruitment of anchovy since 1984 (Hampton 1987) to the current warm phase in the southern Benguela. Although SST is an environmental factor that improves survival (Skud 1982, cited by Shannon *et al.* 1988), SST *per se* may not be the direct cause of changes in fish populations, but rather reflect changes in the environment (Shannon *et al.* 1988).

The high annual occurrence of anchovy in west-coast jackass penguin diet in recent years (Fig. 3.4) may be a consequence of, and hence reflect, good anchovy recruitment: as anchovy recruits migrate inshore along the west coast (Hampton 1987), the availability of these small fish to breeding, foraging jackass penguins increases.

Whereas moderate positive SST anomalities appear to be advantageous to pelagic fish populations (Shelton *et al.* 1985, Shannon *et al.* 1988), exceptionally strong warming may adversely affect year-class strength (Shelton *et al.* 1985). A "warm event" occurred in the southern Benguela in the summer of 1982-83 (Shannon 1983), when unusually high sea temperatures were recorded in the region (Walker *et al.* 1984). This minor warm environmental pertubation, attributed to the interruption of the seasonal upwelling process due to abnormalities in the summer wind regime (Walker *et al.* 1984), had a noticeable impact on the performance of the South African purse-seine fishery (Shannon *et al.* 1984b). Especially anchovy and red-eye landings were affected, resulting in very poor and very good catches of these two species, respectively (Anon. 1983a, Shannon *et al.* 1984b). This apparent decrease in availability of anchovy to the purse-seine fleet in 1983 was, however, not reflected in penguin diet (Fig. 3.4). Although nest desertion of jackass penguins and increased mortality of post-moulting adults occurred during the summer of 1982-83 (Duffy *et al.* 1984), the annual probability of occurrence of anchovy in penguin diet in 1983 was high and similar to other, normal years (Fig. 3.4). This suggests that anchovy were available inshore, close to the west-coast breeding islands.

Berruti & Colclough (1987) hypothesized that the year-class of pilchard spawned during the 1982-83 warm event was relatively strong and isolated in comparison with previous years. The appearance of large pilchard in west coast fishery landings in 1985 (Anon. 1985) supported their prediction of regional increases in pilchard biomass. The biomass increase was, however, not evident from the annual probability of occurrence of pilchard in diet samples of west-coast jackass penguins in 1985, as availability appeared to be average (Fig. 3.5). However, good pilchard landings were made on the west coast since 1985, particularly in 1987 when the pilchard catch reached 27.9×10^3 tons (Sea Fisheries Research Institute, unpubl. data). Further evidence for regional increases in

(Fig. 3.7). This indicated that in those years the availability of these predominant prey species to penguins was high.

As attempts to equate resource abundance with resource use are difficult due to the complexity of factors affecting components of resource systems (cf. Wiens 1984, cf. Fig. 3.16), the patterns in annual absolute abundance of prey items in penguin diet need to be verified, before being interpreted. Trends were considered verified if patterns in diet- and catch-based indices of pelagic fish abundance were identical. However, CPUE as an index of pelagic fish biomass is subject to potential bias (Newman *et al.* 1979; Butterworth 1980, 1988) and should therefore be treated with caution. It was assumed that the abundance of pelagic fish species in penguin diet and the total fishery landings of these species are proportional to the species' actual abundance in the environment. Berruti & Colclough (1987) already showed that, at least at low biomass levels, the abundance of pilchard in Cape gannet diet and fishery landings was correlated.

Because the foraging range of breeding jackass penguins and the fishing area of the commercial purse-seine fishery are largely separate (Wilson 1985a, Wilson *et al.* 1988), and the relative number of prey species other than anchovy in penguin diet is small, the similarity of diet- and catch-based species-year associations indicated that the high proportions of red-eye in 1983 and pilchard in 1987 in penguin diet appeared to be due to an increase in stock size. This shows that the unusually high commercial catches of red-eye in 1983 were not only a response by the commercial fishery to new management rules (Anon. 1983b, Duffy *et al.* 1984), but may have reflected actual increases in availability. The fact that the predominance of red-eye in 1986 and maasbanker in 1984/85 in penguin diet was not reflected in purse-seine landings, suggests that the high availability may have been due to the inshore movement of the fish species, within the penguins' foraging range.

Anchovy size-range

Whereas size-frequency distributions of anchovy taken by west-coast penguins throughout the year provide qualitative descriptions of anchovy length data, the analysis of median lengths allows possible trends in anchovy length to be described quantitatively. The accordance of trends of median length with size-frequency distribution of anchovy confirmed that median length is a good "one-figure summary" of anchovy length-frequency distributions. As such it may be a useful tool in quantifying trends in length, and thus age, of anchovy in seabird diet.

Major changes in the size-frequency distributions and median lengths of anchovy in west-coast jackass penguin diet occurred between 1981-83 (Fig. 3.13) and correspond to the commencement of the warm period (Walker *et al.* 1984) currently experienced. As anchovy are approximately 11 cm long after a year's growth (Prosch 1986), the decreased occurrence of large anchovy (> 100 mm caudal length) in penguin diet after 1984 indicates that foraging jackass penguins at the west coast appeared to take 0-year-old fish almost exclusively after 1984. The good recruitment of anchovy since 1984 (Hampton 1987) was attributed to the current warm phase (Shannon *et al.* 1988) and appears to have resulted in an increased availability of a large number of recruits (see above). This may account for the decrease in anchovy size between 1984 and the relatively constant diet-based annual median lengths in later years. Furthermore, the second wave of small anchovy which appeared in July in 1985-87, but not prior to 1985, suggests sustained recruitment or late spawning in favourable years. This second influx of small anchovy is discussed in chapter five.

Environmental factors presumably affect the pelagic fish population on the whole. If the decrease in anchovy length is due to environmental changes in the southern Benguela, the decrease is predicted to be observed simultaneously by regular, independent samplers of these stocks, eg. jackass penguins and the commercial purse-seine fishing fleet. Not only was the decrease in diet-based annual median lengths reflected in the length of anchovy in fishery catches made around the South African coast during 1983-86, but the rates of decrease were similar as well. As purse-seiners fish primarily offshore for fear of damaging their nets on rocky and irregular bottoms inshore (Duffy *et al.* 1987a), the accordance moreover indicated that the decrease in anchovy length is not due to an inshore movement of juveniles.

The large increase in annual median length of anchovy in fishery landings during the last two years appeared to be the result of the good availability of adults to the fishery on the west coast (Shelton *et al.* 1988). Although larger anchovy also occurred in penguin diet in the first part of the year in 1987-8 than in 1985-6, this increase was not reflected in diet-based medians later in the year. Contrary to the fishery, the number of large fish in penguin diet may not have been sufficiently high to have an impact on the diet-based median, as medians do not take the actual measurement into account but only the rank of the measurement (Zar 1984).

The analysis of long-term trends in the diet of jackass penguins at the west coast showed that the jackass penguin may be used as a qualitative sampler of the marine environment in the southern Benguela, and may provide information complementing other studies. Several of the trends were ascribed to recent environmental changes. Penguin diet indicated that the absolute abundance of anchovy generally increased since 1980, and that prey species other than anchovy did not vary in abundance seasonally. Different prey species did, however, predominate at annual time scales.

The use of the jackass penguin as a quantitative sampler of the marine environment appeared to be limited to the size of anchovy taken. Analyses of penguin diet showed that median anchovy lengths decreased significantly between 1980-88 and that anchovy migration patterns established from catch-dependent and -independent data were clearly manifested in penguin diet. Moreover, penguin diet also reflected anomalous anchovy distribution of 1987-88, indicating that jackass penguins at the west coast "track" anchovy populations. Jackass penguins may therefore provide quantitative information useful in the management of the anchovy resource in the southern Benguela.

3.5 Summary

Trends in monthly and annual prey species composition (frequency of occurrence and abundance) and anchovy size-range (size-frequency distribution and median length) were described from.1 157 stomach samples collected from jackass penguins at the west coast between 1980-88, and analyzed. Penguin diet was numerically dominated principally by anchovy, but maasbanker, cephalopods, red-eye and pilchard were also taken.

Trends in monthly probability of occurrence of anchovy were inverse to those of prey other than anchovy, and reflected limited features of the anchovy migration. However, patterns and variation in the timing of this annual migration, as well as unusual anchovy distributions, were clearly reflected in trends of monthly anchovy size-range. Monthly absolute abundance of alternate prey species to anchovy did not vary seasonally.

Annual probability of occurrence and relative numerical abundance of anchovy in penguin diet was high after 1984. These trends appear to reflect high levels of recruitment and an increase in biomass, respectively, and are attributed to positive SST anomalities recorded in the southern Benguela recently. Different prey species were predominant in different years. Based on coincident trends in diet and fishery landings (CPUE), the high proportions of red-eye and pilchard in 1983 and 1987, respectively, appeared to reflect increased stock size. A significant decrease in the size of anchovy taken by penguins between 1980-88 was observed.

Chapter 4

A COMPARISON OF THE DIET OF JACKASS PENGUINS AT THE WEST AND SOUTHWEST COAST OF SOUTH AFRICA

4.1 Introduction

The jackass penguin is endemic to southern Africa (Clancey 1980) and is the only member of the Order Sphenisciformes breeding on the African continent (Shelton *et al.* 1984). The documented penguin population decline over the last three decades (Crawford & Shelton 1981, Shelton *et al.* 1984) has not been consistent across the species' range. Between 1956 and 1978 the decrease in penguin numbers at colonies on the west coast of South Africa amounted to 38 % (Shelton *et al.* 1984), whereas the populations at the southwest coast colonies increased more than five-fold over the same period (Crawford & Shelton 1981, Shelton *et al.* 1984). Crawford & Shelton (1981) suggested that differences in prey availability between both coasts may precipitate these trends. Here, the diet of west- and southwest-coast penguins is compared for the first time, trends in prey species composition and anchovy size-range being analyzed.

The size of anchovy is an index of their age (cf. Prosch 1986). The traditional distribution model of anchovy off the coast of South Africa (Crawford 1981a) assumes implicitly that recruitment of juvenile fish takes place only on the west coast (Duffy *et al.* 1985). The occurrence of post-larval anchovy in the diet of jackass penguins on the southwest coast (i.e. at Dyer Island), led Duffy *et al.* (1985) to propose an alternative anchovy distribution model in which the region of recruitment is extended to the southwest and south coasts of South Africa. This hypothesis was based on a small data set of penguin diet between 1982-84, and since 1987, the diet of penguins at the southwest coast has been sampled frequently and regularly. The hypothesis of Duffy *et al.* (1985) is here evaluated on the basis of further and more extensive data between 1985-88.

4.3 Results

Trends in the prey species composition and anchovy size-range of west-coast jackass penguin diet were already described in chapter three and further descriptions are only repeated here where relevant.

At Dyer Island, 565 Jackass penguin stomach samples were collected during 21 months between June 1982 and June 1988 (Table 4.1). Only 192 samples were collected before 1987 (Table 4.1). This is a substantially smaller total number than the 892 samples obtained at the west coast during the same period (Table 3.1). Months were not sampled equally frequently (Table 4.1). No stomach samples were obtained in 1986, and in September and December of any year.

4.3.1 Prey composition

<u>Frequency of abundance</u>

A total of 9 599 prey items was obtained from southwest-coast penguin stomach samples during 1982-88, compared to 14 273 prey items obtained from west-coast diet samples during the same period (Table 3.3). Diet samples from the west and southwest coasts do not show significant differences in prey composition; anchovy, pilchard, maasbanker, red-eye and cephalopods were taken by penguins at both localities. At the southwest coast, anchovy numerically constituted 95.8 % of all penguin prey items (Table 4.2). This is a substantially higher proportion than at the west coast, where anchovy constituted 68.2 % of prey items in all diet samples (Table 3.2). Anchovy, pilchard, maasbanker, red-eye and cephalopods accounted for a much higher proportion of prey items in the diet of penguins at the southwest-coast (98.5 %) (Table 4.2) than at the west-coast (76.6 %) (Table 3.2).

Annual relative frequency of numerical abundance of the above prey species in the diet of penguins at the southwest coast are presented in Table 4.3. Whereas the relative frequency of abundance of anchovy in west-coast diet samples varied (Table 3.3), that of anchovy in southwest-coast penguin diet was consistently above 95 % in all years, except in 1984 (Table 4.3). The annual relative abundance of the other prey at the southwest coast were consequently very low (generally < 1 %) and variable (Table 4.3). During 1982–88, highest proportions of pilchard and maasbanker in southwest-coast penguin diet occurred in 1984, and coincided with low anchovy abundance (Table 4.3).

Monthly trends

Combined west- and southwest-coast data were analyzed to identify relative trends in absolute prey abundance in the diet of penguins at both coasts during 1982–88. Similar to the correspondence analysis of west coast penguin diet (section 3.3.1 in chapter three), anchovy dominated the combined monthly diet of jackass penguins at the west and southwest coast and swamped the correspondence analysis; 93.4 % of items constituted by the five most important prey types in penguin diet were anchovy, yet anchovy accounted for only 3.0 % of the total inertia. Hence anchovy were excluded from the analysis but included in the graphical display as a supplementary point. Four months were treated similarly. The first two axes in the correspondence analysis of the combined west- and southwest-coast penguin diet data accounted for 80 % of the total inertia, the same proportion as in the analysis of the west coast data only. The data matrix of monthly prey species composition was completely represented by a third axis.

After anchovy had been excluded from the correspondence analysis, 46.6 %, 23.6 %, 18.8 % and 11.0 % of the remaining prey items were cephalopods, maasbanker, red-eye and pilchard, respectively (Table 4.4). Maasbanker, cephalopods and, to a lesser extent, pilchards are almost completely represented in the two-dimensional display, whereas red-eye is poorly represented (Table 4.4).

The first two dimensions (principal axes) of the correspondence analysis of monthly combined west- and southwest-coast penguin diets are shown for all months in Figure 4.1. Two features of the two-dimensional graphical display of the penguin diet data matrix are evident. Firstly, no pattern in the months with a high proportion of one or more particular prey species was evident either at the west coast, or at the southwest coast (Fig. 4.1). Secondly, a high proportion of pilchard, and low proportion of cephalopods, occurred mainly in monthly diet samples of southwest-coast penguins (Fig. 4.1). The opposite trend was evident in west-coast diet samples: low proportions of proportion of anchovy less than 60 mm in caudal length in monthly penguin diet was smaller at southwest than at the west coast (Table 4.5).

Similar to the west coast, inter-annual monthly size-frequency distributions of anchovy in southwest-coast penguin diet were heterogeneous, overall significant differences occurring in all months (Table 4.6). Thus monthly anchovy length data of the same month in different years could not be justifiably pooled. Statistical analyses of inter-annual monthly trends were therefore not possible.

Annual trends

Similar to the west coast, there was a significant overall difference in the annual size-frequency distributions of anchovy taken by southwest-coast jackass penguins between 1982-88 (df = 40, χ^2 = 4799, P < 0.0001). During that period, size distributions showed a clear shift in emphasis from predominantly large (> 90 mm) to smaller fish (Fig. 4.6).

Median lengths

Monthly trends

In 15 out of 18 months between 1983-88, monthly median lengths of anchovy in southwest-coast penguin diet were significantly larger than those of anchovy taken by jackass penguins at the west coast (Table 4.7).

Similar to the west coast, pooling of southwest-coast inter-annual monthly median lengths was not justified, as overall significant differences occurred in January to November (Table 4.6). Statistical analyses of these median lengths were therefore not possible.

Annual trends

Annual median caudal lengths of anchovy in southwest-coast penguin diet decreased from 109 mm to 80 mm between 1982 and 1988 (Fig. 4.7). This reflects the decrease in anchovy length observed in annual size-frequency distributions (Fig. 4.6). Simple linear regression of annual anchovy median length on year between 1983-88 was not significant (b = -4.3 mm year^{-1}, df = 1,4; F = 6.25, $P > 0.05$, $r^2 = 0.61$). Simple linear correlation between annual median lengths of anchovy in west- and southwest-coast penguin diet was also not significant (df = 3, r = 0.25, $P >> 0.05$). Annual median lengths of anchovy taken by jackass penguins at the southwest coast were significantly larger than those taken by west-coast penguins and in total South African commercial fishery catches (Fig. 4.7).

4.4 Discussion

Monthly trends

Frequency of abundance

Before the collapse of the pilchard fishery in the mid 1960s, pilchard was the dominant and thus preferred prey species of jackass penguins (Burger & Cooper 1984). Crawford & Shelton (1981) indicated that due to increased fishing pressure on younger age groups, adult pilchards (aged two or older) were only available to seabirds east of Cape Point. They thus suggested that the availability of adult pilchard in the vicinity of Dyer Island may have resulted in a shift of penguins from the west coast to the southwest coast, precipitating the divergent population trends observed (Crawford & Shelton 1981). This implies that pilchard should be well represented in the diet of southwest-coast penguins. However, comparisons of relative numerical abundance of the five most important prey species in the diet of west- and southwest-coast jackass penguins clearly showed that anchovy was the principal prey species of penguins at both localities during 1982–88 (cf. Tables 3.2, 4.2). Furthermore, anchovy dominated the diet of penguins to a greater extent at the southwest than at the west coast. Nevertheless, pilchard appeared to be relatively more abundant in monthly southwest- than in west-coast penguin diet during 1987–88 (Fig. 4.1). Whether this trend is due to recent increases in pilchard biomass (Anon. 1985, Berruti & Colclough 1987), or due to possible biases resulting from more frequent diet sampling in 1987–88 compared to earlier years (Table 4.1), is difficult to say.

A comparison of the diet of jackass penguins at the west (1980-88), southwest (1982-88) and east coast (1979-81) (Randall & Randall 1986) shows that red-eye were more abundant at the east coast than at the other two localities (Table 4.8). Relative abundance of cephalopods in east- and southwest-coast penguin diets was similar, but lower than at the west coast (Table 4.8). Pilchard were relatively more abundant in east-coast diet than at the other sites (Table 4.8), as implied by Crawford & Shelton (1981). Moreover, pilchard was the second most important prey species after anchovy in terms of reconstituted mass at the east coast, where no pelagic fishery exists (Randall & Randall 1986). Length measurements of species other than anchovy are not available for the west and southwest coasts and therefore comparisons of reconstituted mass are not possible. However, the small number of small anchovy and less variable anchovy size in southwest-coast jackass penguin diet suggests that the importance of anchovy to penguins at the southwest coast is unlikely to be overestimated on a numerical basis (cf. Duffy & Jackson 1986, chapter three).

No seasonal patterns in the prey species composition (excluding anchovy) occurred in neither west- nor southwest-coast penguin diet (Fig. 4.1). This is consistent with, and similar to, the result of the west-coast data analysis (chapter three) and indicates that none of the prey species exhibit seasonal peaks of abundance in penguin diet at either coast.

Frequency of occurrence

The trends in monthly frequency of occurrence of anchovy in penguin diet suggest that during 1987-88 anchovy were available more consistently at the southwest than at the west coast (Figs 4.2 - 4.3). Availability of west-coast anchovy during April - August 1987 appeared to be lower and more variable than during the rest of the year. This appears to be due to independent fluctuations, consistent neither between years nor localities (Figs 4.2 - 4.3). Furthermore, pilchard appear to undergo between-year fluctuations in availability to penguins at the west and southwest coast during 1987-88. This is in contrast to cephalopods, which appear to exhibit a consistently higher availability at the west than at the southwest coast (Figs 4.2 - 4.3).

<u>Anchovy size-range</u>

Anchovy are believed to spawn off the south coast of South Africa (Crawford 1981a), eggs and larvae being transported by a sub-surface frontal "jet current" northwards to the nursery area in the St Helena Bay region at the west coast (Shelton & Hutchings 1982). Nought-year old fish generally occur off the west coast and then migrate in a southerly and easterly direction to return to the Agulhas spawning area (Crawford 1981a). Thus maturing recruits and larger one- and two-year old fish are found on the southwest coast, east of Cape Point (Crawford 1981a, Hampton 1987). The occurrence of larger anchovy of less variable size-classes at the southwest than at the west coast (Table 4.7, Figs 3.10 - 3.11, 4.4 - 4.5) is consistent with the model of anchovy distribution of Crawford (1981a). The diet of breeding, adult jackass penguins at the west and southwest coast therefore reflects migration and distribution patterns of anchovy.

The occurrence of 30-35 mm anchovy in the diet of jackass penguins at Dyer Island, led Duffy *et al.* (1985) to conclude that recruitment must have occurred locally, as such small fish could not have completed the St Helena - Dyer Island round-trip within the short period suggested by their age. The occurrence of less than 25 mm anchovy in southwest-coast penguin diet in August 1987 (Fig. 4.5) suggests that local recruitment did take place at the southwest coast. This is in contrast to the traditional model of anchovy distribution. Based on the larger proportion of recruits (anchovy < 60 mm in caudal length (Duffy *et al.* 1985)) in the diet of west- than southwest-coast jackass penguins (Table 4.5), the relative strength of recruitment appears to be consistently larger at the west than at the southwest coast.

Annual trends

<u>Frequency of abundance</u>

In contrast to the west-coast, the annual relative abundance of anchovy in southwest-coast penguin diet did not decrease during the warm event of 1982-3, when food shortages were experienced by birds at the west coast (Duffy *et al.* 1984), but only in 1984 (Tables 3.3, 4.3). This supports the assertion of Duffy *et al.* (1984) that during 1982 anchovy were available east of Cape Point.

Contrary to trends at the west coast, the relative annual abundance of anchovy in southwest-coast penguin diet remained constant after 1984 (Tables 3.3, 4.3). This suggests that the abundance of anchovy at the southwest coast has been relatively constant, despite increased levels of anchovy recruitment since 1984 (Shelton *et al.* 1988).

<u>Anchovy size-range</u>

Trends in median caudal length were in accordance with size-frequency distributions of anchovy (Figs 4.6, 4.7; cf. chapter three). Median lengths of anchovy taken by penguins at the southwest coast were usually larger than medians of anchovy in fishery landings, which in normal years consist of approximately 80 % of anchovy recruits by number (Shelton *et al.* 1988). This suggests that southwest-coast penguins are less dependent on anchovy recruits directly for a predictable food supply than are west-coast penguins. Penguin populations at the southwest coast may therefore be less affected by changes in anchovy recruitment patterns than west-coast ones.

A shift from large to smaller anchovy is evident in the diet of penguins at both the west and southwest coasts (Fig. 4.7). At the southwest coast this change appears to have taken place between 1985 and 1987 (Fig. 4.6), later than at the west coast (Fig. 3.13). This may just reflect the less intensive sampling of penguin diet prior to 1987 at the southwest than at the west coast (cf. Table 3.1, 4.1).

Decreases in anchovy size have occurred in the diet of penguins in two different areas, as well as commercial purse-seine landings, further substantiating the conclusion that the decrease in anchovy length observed in jackass penguin diet is not due to inshore movements of juveniles (chapter three). As southwest-coast penguins take a smaller proportion of small anchovy than do west-coast penguins, the decrease in length of anchovy in southwest-coast penguin diet cannot be attributed to better recruitment and hence higher availability of small anchovy, as was done for the west-coast trends (chapter three). This indicates that more complex mechanisms other than environmental temperature anomalities may be responsible for the observed changes in anchovy length in the southern Benguela.

Comparison of the diet of jackass penguins at the west and southwest coast showed that although the same prey species were taken by birds at both localities, subtle differences in diet were apparent. Whereas the numerical abundance of pilchard was higher in southwest-coast diet, anchovy numerically dominated the diet of penguins at both localities, particularly at the southwest coast. The consistent occurrence of larger anchovy of smaller size-variability at the southwest coast, and the existence of possibly larger fluctuations in monthly anchovy availability at the west coast, suggests the presence of a large stock of anchovy throughout the year at the southwest coast. This may result in better survival of jackass penguin chicks and/or juveniles at the southwest coast.

The size of anchovy taken by jackass penguins at both coasts clearly reflects anchovy migration and distribution patterns. Based on the proportion of small anchovy in penguin diet, anchovy recruitment appears to be at a much smaller scale at the southwest than at the west coast.

4.5 Summary

Trends in monthly and annual prey species composition (frequency of occurrence and abundance) and anchovy size-range (size-frequency distribution and median length) were described from 565 stomach samples collected from jackass penguins at the southwest coast between 1982-88, and compared to those obtained from west-coast penguin diet. Comparisons of the last two years are emphasized. Diet samples from penguins at the west and southwest coast did not appear to show significant differences in prey composition. Anchovy was the principal prey species at both localities but dominated penguin diet to a greater extent at the southwest than at the west coast.

During 1987-88, the availability of anchovy appeared to fluctuate independently at the west coast, whereas it was consistently high at the southwest coast. Absolute abundance of prey species other than anchovy did not vary seasonally in southwest-coast penguin diet. However, pilchard and cephalopods were more

abundant at the southwest and west coast, respectively. Anchovy taken by southwest-coast penguins were consistently larger and less variable in size than those at the west-coast. Penguin diet was shown to reflect general anchovy distribution and migration patterns. Local anchovy recruitment occurred at the southwest coast in 1987, but the relative recruitment strength appeared to be larger at the west than at the southwest coast. Decreases in the size of anchovy taken by penguins at both localities were coincident. More complex mechanisms other than environmental temperature anomalities may be responsible for changes in anchovy length observed in the southern Benguela.

Chapter 5

JACKASS PENGUINS AS MONITORS OF ANCHOVY RECRUITMENT?

5.1 Introduction

Clupeoid stock size is generally very dependent on year-to-year recruitment (Blaxter & Hunter 1982). It has been asserted that the lack of strong density-dependent population regulatory mechanisms results in extreme natural recruitment variability of these stocks (Cushing 1971b). This variability, combined with a short life-span and high natural mortality (Blaxter & Hunter 1982), results in clupeoid stocks being susceptible to overfishing (Cushing 1971b).

In the southern Benguela region, Cape anchovy *Engraulis capensis* has been consistently the major contributor to catches of the South African purse-seine fleet since 1966 (Crawford *et al.* 1987). Anchovy landings are dominated by recruits (Hampton *et al.* 1985), the anchovy catch in normal years consisting of about 80 % recruits by number (Shelton *et al.* 1988). Juvenile anchovy recruit to the fishery from February/March onwards and become most readily available in June (Crawford 1981a, Crawford *et al.* 1987). Since 1985, advice for the management of this important renewable resource has been based on information obtained from direct surveys of spawner and recruit biomass, which employ acoustic and egg-production methods (Hampton *et al.* 1985, Hampton 1987).

Cape anchovy is the principal prey of jackass penguins *Spheniscus demersus* (Wilson 1985a, Duffy *et al.* 1987a) which breed on 12 South African islands in the southern Benguela region (Shelton *et al.* 1984). The jackass penguin accounts for 27.8 % of the total resident breeding seabird biomass in the region (Duffy *et al.* 1987b), and is the only seabird breeding throughout the year at localities adjacent to the annual anchovy migration route (Berruti 1987, Crawford *et al.* 1987). Duffy *et al.* (1985) showed that small anchovy are eaten by jackass penguins earlier in the year than they appear in commercial landings, and have suggested that annual variations in timing and strength of anchovy recruitment may be detected by monitoring the diet of jackass penguins along the west coast.

The use of west-coast jackass penguins as monitors of timing and strength of anchovy recruitment was assessed by examining penguin diet over the periods 1981-88 and 1985-88, respectively. The hypothesis that abundance of small anchovy in penguin diet is directly proportional to recruitment strength was tested at local and regional spatial scales. Throughout this chapter, the term recruitment is used in the population, and not in the fisheries, context, i.e. recruitment is the addition of young individuals to the population.

5.2 Methods

General methods of data collection and analyses are described in chapter two. During January 1981 and February 1987 field work was conducted on Marcus Island (33° 02′S, 17° 58′E). To reduce pressure on the small penguin population on Marcus Island, subsequent field work was carried out on Jutten Island (33° 05′S, 17° 57′E). As the two islands lie only *c.* 4 km apart (Fig. 1.1), diet samples collected at either island were regarded as reflecting the west-coast condition as a whole.

Monthly length-frequency distributions of anchovy in jackass penguin stomach samples during 1981-88 were calculated. Since only 11 diet samples were collected in 1982, that year was excluded from all analyses. Timing of recruitment was determined by identifying the month in every year in which the largest proportion of small anchovy occurred in penguin diet. Catch-independent estimates of recruitment, determined from direct surveys employing acoustic methods (Hampton 1987), were correlated to the percentage (by number) of small anchovy occurring annually in west-coast penguin diet. Small anchovy were considered to be fish with a caudal length less than 56 mm (cf. Table 1, Smith 1985), an age of approximately four months (Prosch 1986).

Acoustic surveys are conducted along the southern African coast in a stratified random grid (Hampton 1987). Acoustic recruitment estimates for the survey stratum corresponding to the coastal area off Saldanha Bay, and total annual estimates, were used for testing the hypothesis at local and regional spatial levels, respectively.

Moreover, fine and micro local spatial scales were achieved by respectively distinguishing between combined inshore-offshore recruitment biomass estimates per stratum, and inshore estimates only. Recruitment estimates for individual strata of surveys in 1985-6 and 1987-8 were obtained from Hampton (Tables 3 and 5, 1987) and the Sea Fisheries Research Institute (M.J. Armstrong, pers. comm.), respectively (Table 5.1). Acoustic estimates of total annual anchovy recruitment derived from direct surveys conducted in 1985 - 1987 and 1988 were obtained from Shelton *et al.* (1988) and the Sea Fisheries Research Institute (I. Hampton, pers. comm.), respectively. For comparisons at regional scales, jackass penguin diet was integrated over different annual periods, viz. January - February, January - March, January - April, etc.

5.3 Results

A summary of jackass penguin diet samples collected during 1981-88 (eg. mean number of monthly/annual samples, etc.) is given in section 3.3 of chapter three and in Table 3.1. During that period a total of 12 240 anchovy length determinations were made. Between 1985 and 1988, the mean (± 1 SD) number of monthly stomach samples collected during January and July was 17.5 (± 8.9). A total of 6 565 anchovy were measured. The mean (± 1 SD) number of caudal length determinations made over each January - July period was 1 641 (± 374).

During 1981 and 1988, an influx of small anchovy occurred annually in west-coast jackass penguin diet (chapter three). Timing of anchovy recruitment was very variable (chapter three, Figs 3.10 - 3.11), but successful reproduction appeared to have occurred in all years. The month in which the annual maximum proportion of small anchovy in penguin diet occurred varied between February and June (Table 5.2). However, in four out of the seven years examined, recruitment occurred in March or April (Table 5.2). In 1985, an unusual second annual influx of small anchovy occurred in July (Fig. 3.10). The maximum percentage of anchovy smaller than 56 mm varied between 21.3 and 62.9 % (Table 5.2).

Between 1985-88, acoustic recruit biomass estimates at the fine local spatial scale were not significantly correlated to the percentage of small anchovy occurring in the diet of west-coast penguins in the month in which the surveys took place (df = 2, r = 0.34, $P > 0.05$). The correlation coefficient between direct recruit estimates of inshore survey strata only, and small anchovy in penguin diet was much larger, and negative, at this micro spatial scale than at the fine one. However, the relationship was not significant (df = 2, r = −0.86, $P > 0.05$).

At the regional spatial scale, a significant negative correlation (df = 2, r = −0.994, $P < 0.01$) between acoustic estimates of annual anchovy recruitment and the percentage of anchovy < 56 mm in caudal length in the diet of west-coast jackass penguins between January and July each year, existed (Fig. 5.1). Simple linear correlations for shorter annual periods (eg. January - March, January - April, etc.) were not significant (Table 5.3).

5.4 Discussion

Underlying the interpretation of trends in the size of anchovy taken by jackass penguins are two assumptions. Firstly, that migration and distribution patterns of anchovy are reflected in penguin diet. The validity of this assumption has been verified in chapters three and four, respectively. Secondly, that the proportion of anchovy size-classes in penguin stomach samples reflect actual proportions in the environment. A shift to larger anchovy taken by jackass penguins during a period of unusually high availability of adult anchovy off the west-coast in 1987-8 (Shelton *et al.* 1988) was demonstrated in chapter three. This suggested that penguins preferentially prey on larger fish than on smaller ones. As southward migrating anchovy recruits are concentrated close inshore - in 1985-6 mainly within 15 km of the coast (Hampton 1987) - recruits are distributed within the 24.2 km maximum theoretical foraging range (Wilson 1985a) of breeding jackass penguins. Thus the appearance of small anchovy in penguin diet indicated that comparatively few large or adult fish were available to penguins within their foraging range. For the purpose of monitoring anchovy recruitment, interpretations of quantified trends of the size of anchovy taken by jackass penguins can be regarded as unrestricted by the relative, rather than absolute, nature of proportions of different anchovy size-classes.

Timing of recruitment

Continued commercial fishing in the event of reproductive failure may lead to the collapse of the exploited fish stock. Duffy *et al.* (ms) proposed that delayed recruitment may suggest reproductive failure. Examination of the timing of recruitment may, firstly, allow the variability in timing to be estimated and, secondly, delayed recruitment to be identified in future years. Knowledge of recruitment success may allow fisheries managers to take effective tactical measures timeously, i.e. before a drastic stock decrease or collapse occurs.

Anchovy less than 56 mm in caudal length occurred in west-coast jackass penguin diet in more than one month each year (Figs 3.10 - 3.11). To detect delayed recruitment, the proportion of small anchovy in penguin diet constituting recruitment needs to be quantified. The smallest annual maximum proportion over the eight-year period examined was 21.3 % (Table 5.2). It is therefore suggested that if 20 % (by number) of anchovy caught by west-coast jackass penguins in one particular month are less than 56 mm in caudal length, recruitment is considered to have occurred.

If the usual timing of recruitment is taken to be April/March, the influx of small anchovy in penguin diet only in May 1983 and June 1988 indicated delayed recruitment and thus possible reproductive failure. However, fishery catches in 1984 were normal (Crawford *et al.* 1987), and the 1988 acoustic recruitment estimate was high compared to previous years (Shelton *et al.* 1988). Thus anchovy reproduction appeared to be successful despite apparent late recruitment.

Recruitment patterns may be influenced by spawning behaviour (Crawford 1981a). Anchovy are serial spawners, the main spawning season in the southern Benguela extending from October to February (Shannon & Pillar 1986). The spawning by first-year fish between October and December is primarily responsible for the large number of eggs observed during that period (M.J. Armstrong pers. comm., Shelton *et al.* 1985). Older fish spawn as well but later, and their contribution is believed to be of much less significance than that of recruits (M.J. Armstrong, pers. comm.). The number of individuals remaining from a spawn is the result of several mortality rates (Lasker 1985) affecting different stages in the life cycle of anchovy differently (Smith 1985). Natural mortality in individuals occurs from predation, starvation, disease and abiotic factors (Lasker 1985). If it is assumed that levels of egg, larval and juvenile mortality are constant throughout any one year, it may be possible to deduce spawning behaviour from patterns in the timing of recruitment. As anchovy length is an index of age (Prosch 1986), the birthdate of anchovy can be calculated. Wave(s) of small anchovy occurring in penguin diet may thus be related to spawning peak(s). Recruitment in different years occurred in February, April/March and June (Table 5.2), indicating that the birthdate for 55 mm anchovy was November, January and February, respectively. Birthdates derived from anchovy in penguin diet thus correspond to the spawning season determined by direct plankton sampling (Shelton *et al.* 1985, Shelton 1986). The appearance of anchovy less than 25 mm, an age of approximately 30 to 60 days (Prosch 1986), in penguin diet in September 1987 (Fig. 3.11) suggested that some spawning occurs as late in the year as July. Furthermore, the influx of small anchovy in July 1985, and to a lesser extent in 1986-87 (Fig. 3.10), indicated that an unusual second spawning peak had occurred in the previous spawning season. This may have been the result of some recruits spawning later than usual or, alternatively, the spawning of older fish.

Strength of recruitment

Various studies have demonstrated relationships between variables of seabird biology and fish stocks important to fisheries (cf. Nettleship *et al.* 1984). However, only few studies have demonstrated statistical relationships (eg. Anderson *et al.* 1982, Hislop & Harris 1985, Monaghan & Zonfrillo 1986, Montevecchi *et al.* 1988). The present study is the first to show a statistical relationship between pelagic schooling fish abundance in seabird diet and biomass of that particular prey, directly. As it is not justified to equate resource availability to resource abundance (Wiens 1984, commercial fishery catch statistics do not accurately reflect anchovy abundance in the environment. Here the use of catch-independent recruitment data introduced an element of "ground-truthing" to the comparisons of the proportions of small anchovy, and allowed calibration of penguin diet to actual resource abundance. Berruti & Colclough (1987) ascertained such a relationship indirectly by demonstrating a significant correlation between commercial catches of pilchard *Sardinops ocellatus* in the western Cape, and the abundance of pilchard in the diet of Cape gannets *Morus capensis*. They concluded that commercial pilchard catches and pilchard abundance in gannet diet are both directly related to pilchard biomass when the latter is low.

Jackass penguins have a near-shore distribution (Wilson 1985a) and therefore tend to forage on shoals of pelagic fish distributed within the 200 m contour (Crawford 1980). Because anchovy recruits are distributed close inshore (Hampton 1987), the better correlation between penguin diet and direct recruitment estimates of the inshore stratum, as opposed to that of combined inshore-offshore strata, is expected. The opposite sign of the coefficients of the two correlations at the local spatial scale may be a consequence of the small sample size involved and the large variance of the 1985-6 direct recruit biomass estimates (Tables 3 and 5, Hampton 1987).

Shelton *et al.* (1988) showed that the high availability of adult anchovy on the west coast during 1987-8, but particularly in 1987, resulted in a larger proportion of adults being caught by the commercial fishery than in 1985-6. In 1987 the percentage of recruits in landings was only 41 % by number, instead of the usual 80 % (Shelton *et al.* 1988) of previous years. This indicated that the impact of fishing on recruits was reduced. Consequently, the escaping biomass of recruits was higher than in normal years, yielding higher recruitment strength estimates than in previous years (Shelton *et al.* 1988).

Jackass penguins presumably maximize the energetic gain of foraging. Under conditions of high adult anchovy availability, penguins would be expected to forage preferentially on large, adult fish, rather than on smaller ones. This appeared to be the case in 1987-8 (Fig. 3.12). Thus high anchovy recruit biomass resulted in a reduced proportion of small anchovy in penguin diet. The consistently negative coefficients of correlation at the regional spatial scale may be a consequence of the synergistic effect of small sample size and anomalous anchovy distribution.

Anchovy eggs and larvae are generally transported farther north than Saldanha and St Helena Bay (Shelton & Hutchings 1982). Thus southward migration of juvenile anchovy occurs past the west-coast penguin colonies throughout the first part of the year. Jackass penguins are able to feed on these recruits during this period. By integrating penguin diet over longer annual periods, the actual abundance of recruits in the environment, i.e. the total recruit biomass, is more accurately reflected in penguin diet. It is thus expected that direct recruitment biomass estimates at regional spatial scales correlate better with the proportion of small anchovy in penguin diet integrated over longer time intervals. Similar to this study, gannet diet reflected regional, but not local, changes in fish biomass (Berruti & Colclough 1987). Moreover, no correlations between fishery catches and gannet diet at monthly time-scales were demonstrated.

Results of correlations at the regional spatial scale have important implications for the concept of jackass penguins as recruitment strength monitors. The absence of significant correlations at short annual intervals indicates that, using the present approach, jackass penguin diet cannot be used to estimate the strength of anchovy recruitment early in the fishing season. However, the significant correlation between acoustic estimates of anchovy recruitment and the proportion of small anchovy in penguin diet during January - July suggests that penguins can be used to obtain information on anchovy populations that may complement other studies. For example, anchovy production is known to occur inshore (Hewitt & Brewer 1983) but the vessel used in current direct surveys in southern African coastal regions is restricted to distances farther than 3 km from the coast (Berruti 1987). Since anchovy school by size (Crawford 1981a), differences in size-frequency distributions of anchovy obtained simultaneously from survey trawls and penguin diet may indicate the existence of unsampled fish schools farther inshore than 3 km. Moreover, anchovy age determination is routinely carried out by the Sea Fisheries Research Institute (M.J. Armstrong, pers. comm.), using otolith growth ring measurements (cf. Prosch 1986). The age of anchovy in west-coast jackass penguin diet may verify unusual birthdates, and thus spawning periods, deduced by other methods.

Monitoring of west-coast jackass penguin diet can clearly provide information on timing of anchovy recruitment. Although timing of recruitment was easily identified, annual anchovy recruitment appeared to be highly temporally variable. Therefore, it is difficult to establish whether recruitment in any one year is delayed or not. The assessment of jackass penguins as monitors of the strength of anchovy recruitment is based on a time series of unusual anchovy distribution. However, different conclusions may be reached in "normal" years. Whereas direct measurements of recruitment are only available from 1985 onwards, penguin diet data go back further and the use of penguins as recruitment strength monitors during normal years cannot be assessed at this stage. While it is not suggested that the commercial anchovy fishery in the southern Benguela is managed on the basis of penguin diet alone, results presented here suggest that west-coast jackass penguin diet can complement information on which advice for the management of this important renewable resource is currently based.

5.5 Summary

Quantified trends in the occurrence of small anchovy in the diet of jackass penguins at the west coast between 1981-88 were used to determine the timing of anchovy recruitment. Timing was highly variable, but generally occurred in March/April. Despite late recruitment in some years, anchovy reproduction appeared to be successful. Unusual spawning dates were observed.

The hypothesis that the abundance of small anchovy in west-coast penguin diet is directly proportional to anchovy recruitment strength was tested at regional and local spatial scales, as well as at different temporal scales. Penguin diet reflected regional, but not local, changes in recruit biomass. Correlations between the abundance of small anchovy in penguin diet and hydroacoustic estimates of recruitment strength were only significant at long annual periods. Using the present approach, jackass penguins cannot be used to estimate the strength of anchovy recruitment early in the fishing season. They can, however, be used to obtain information on anchovy populations that complement other studies.

SUMMARY AND SYNTHESIS

This section attempts to summarize the main findings of the thesis. Statements are not referenced here if they are substantiated elsewhere in the thesis.

Long-term diet trends of west-coast jackass penguins

During 1980-88, the diet of jackass penguins at the west coast was numerically dominated by anchovy, but maasbanker, cephalopods, red-eye and pilchard were also taken. Monthly probability of occurrence of prey other than anchovy in penguin diet increased with decreasing probability of occurrence of anchovy, indicating that the occurrence of alternate prey was dependent on the absence/presence of anchovy. The overall trend of anchovy availability exhibited in penguin diet was inconsistent with the anchovy migration pattern, but as annual migration patterns are variable, it is unlikely that such patterns would be reflected in monthly probability values averaged over the period 1980-88. Availability of anchovy to penguins was lowest in November, when anchovy have been shown to begin spawning over the Agulhas Bank on the southwest coast. Peak availability to penguins coincided approximately with that of anchovy recruits to the commercial fishery. This indicates that certain features of anchovy migration are reflected in availability patterns of anchovy in west-coast penguin diet.

Similarities in trends of monthly probability of occurrence of anchovy obtained from short and long data series indicated that a pattern of availability of anchovy to penguins exists at the west coast, and appears to reflect anchovy migration. However, differences in trends suggest that the timing of annual anchovy migrations is variable. This was further supported by the heterogeneity of inter-annual monthly size-frequency distributions and median lengths of anchovy taken by penguins.

Although monthly absolute abundance of alternative prey species to anchovy in west-coast penguin diet did not vary seasonally, different prey species were predominant in penguin diet in different years. The determination of the relationship between relative abundance of a species in the diet, and absolute abundance of the same species in the environment, requires comparative data on the absolute abundance of other prey species (cf. Berruti 1987), and in practice it is impossible to test this relationship directly (Newton 1980, cited by Berruti 1987). On the basis of coincident trends in abundance of species in penguin diet and fishery landings, the high proportions of red-eye in 1983 and pilchard in 1987 in penguin diet appeared to be due to increased stock size. Similarly, high relative proportions of red-eye in 1986 and maasbanker in 1984/85 were attributed to inshore movements of these fish species because of discordance between diet- and fishery-based trends.

The increase in relative numerical abundance of anchovy in penguin diet during 1980-88 was coincident with anchovy stock increases estimated by direct hydroacoustic measurements, and suggests a real increase in anchovy biomass. The high annual probabilities of occurrence of anchovy in west-coast jackass penguin diet since 1984 appear to reflect high levels of anchovy recruitment recorded in the southern Benguela since 1984. Adverse effects on year-class strength due to the exceptionally strong environmental warming of the 1982-83 "warm event" were not observed in the availability of anchovy to penguins at the west coast. Reported increases in pilchard biomass in 1985 were not reflected in penguin diet. Nevertheless, the unusually high occurrence of pilchard in the diet of penguins in 1987 is coincident with good commercial pilchard catches, and indicates a regional increase in pilchard biomass.

Annual anchovy migration patters were clearly reflected in both monthly size-frequency distributions and median caudal lengths of anchovy in penguin diet. Consistent shifts to smaller size classes were observed in the first part of 1981-88, indicating a distinct seasonal annual wave of small anchovy. Length distributions of anchovy taken by west-coast penguins during the first part of the year in 1987-88 showed a shift to larger anchovy, a trend not previously observed in, for example, 1985-86. This appeared to reflect the unusually high availability of adult anchovy detected at the west coast during 1987-88 from direct surveys and also indicated that anomalous anchovy distributions appear to be reflected in penguin diet.

Between 1980 and 1988, the size of anchovy taken by jackass penguins at the west coast decreased significantly. The decrease was attributed to high anchovy recruitment levels due to positive sea-surface temperature anomalities observed in recent years. As recruits migrate close inshore, environmental change appears to have resulted in the increased availability of recruits near breeding localities. This decreasing length trend was also observed in anchovy in fishery catches, and suggests that the trend is real.

Comparison of west- and southwest-coast jackass penguin diet

The diet of jackass penguins at west and southwest coasts between 1982-88 was compared. Diet samples from the west and southwest coast did not appear to show significant differences in prey composition; anchovy, pilchard, maasbanker, red-eye and cephalopods being taken by penguins at both localities.

Anchovy was the principal prey species of penguins at both localities, but dominated the diet of penguins at the southwest coast to a greater extent than at the west coast. Excluding anchovy, no seasonal pattern in the species composition of alternate prey of penguins at either coast was evident. This indicates that jackass penguins at both coasts are dependent on anchovy as a major food source.

During 1987-88, the monthly frequencies of occurrence, and thus availability, of anchovy in penguin diet were consistently high at the southwest coast, but appeared to fluctuate independently at the west coast. Monthly frequencies of occurrence of other prey species were low at both localities.

Anchovy taken by southwest-coast penguins were consistently larger and less variable in size than those in the diet of west-coast penguins. This is in accordance with the current anchovy distribution model and indicates that jackass penguins reflect general anchovy distribution and migration patterns. Comparisons of the size-classes of anchovy taken by penguins indicate that birds at both coasts mainly take nought-year old fish, but that penguins at the southwest coast forage on slightly older anchovy. Penguins breeding at the southwest coast may be less affected by changes in anchovy recruitment patterns than their west-coast conspecifics.

The dietary importance of pilchards to penguins at breeding localities along the South African coast increased in a west-to-east direction. This is in agreement with predictions of the hypothesis that the differential availability of pilchard to birds may have precipitated the divergent trend in jackass penguin populations at South African offshore islands.

The occurrence of anchovy less than 25 mm in southwest-coast penguin diet in 1987 suggested local recruitment had taken place. This is in contrast to the traditional model of anchovy distribution and supports findings by Duffy *et al.* (1985). However, the relative strength of recruitment appears to be consistently larger at the west than at the southwest coast.

Consistently high frequencies of annual relative abundance of anchovy in southwest-coast penguin diet appear to indicate that high levels of recruitment since 1984 have resulted in a larger proportion of recruits becoming available to spawn on the southwest coast than in previous years.

The coincident decrease in annual median caudal lengths of anchovy taken by penguins at the west and southwest coast, as well as by the commercial fishery, indicates that more complex mechanisms than higher levels of recruitment due to environmental temperature anomalities, may be responsible for the decrease in anchovy length observed in the southern Benguela.

Jackass penguins as monitors of anchovy recruitment

Jackass penguins can clearly provide information on timing of anchovy recruitment. Between 1980–88, anchovy recruitment generally occurred in March/April, but was found to be highly temporally variable. This makes identification of delayed recruitment difficult. However, timing of recruitment later than in March/April did not appear to result in reproductive failure. Back-calculation of anchovy lengths to birthdates showed that unusual spawning times and peaks had taken place.

Between 1985–88, a significant direct relationship between the relative abundance of small anchovy in penguin diet, and actual resource abundance, was demonstrated. The proportion of small anchovy taken by penguins reflected regional but not local changes in recruitment strength. Results of correlations at different temporal scales showed that, using the present approach, jackass penguin diet cannot be used to estimate the strength of anchovy recruitment early in the fishing season.

Conclusions

Jackass penguins prey on commercially important pelagic shoaling fish species in the southern Benguela. Penguin diet was shown to provide potentially useful information about availability, abundance and distribution of these marine resources. The diet of jackass penguins is dominated by Cape anchovy; qualitative changes and quantified trends in the above parameters are, therefore, largely, but not exclusively, limited to this fish species.

Prey composition and, in particular, anchovy-size range, showed that jackass penguins "track" anchovy populations: anchovy migration and distribution patterns, as well as unusual distributions, were reflected in penguin diet. This justifies quantification of trends in distributional ecology of anchovy taken by jackass penguins. To establish whether or not jackass penguins track populations of other pelagic fish species in the southern Benguela which exhibit age-specific distributions (Crawford *et al.* 1987), further investigations are required which determine and take these species' size and age compositions into account.

It is unlikely that seabird data will be included in the information on which pelagic fish resources are managed - at least until techniques for using qualitative data are developed (Berutti 1987). Nevertheless, information about availability, abundance and distribution of anchovy (and, to a lesser extent, other commercially important penguin prey species), can substantiate trends determined through other studies. In addition, penguin diet data can complement information on which current advice for management of the commercial fishery is based. Therefore, as a sampler of the marine environment, the jackass penguin can aid managers of renewable pelagic fish resources in the southern Benguela.

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Table 3.1. The number of monthly stomach samples collected from jackass penguins at the west coast (Marcus and Jutten Islands) during 1980–88

	1980	1981	1982	1983	1984	1985	1986	1987	1988	Total	Mean	SD
Jan	-	29	-	-	-	12	2	20	9	72	14.4	10.4
Feb	-	38	-	15	20	16	20	10	13	132	18.9	9.2
Mar	-	43	9	29	15	18	11	17	9	151	18.9	11.7
Apr	-	39	-	24	20	20	20	20	16	159	22.7	7.5
May	-	37	11	33	18	20	10	36	20	179	22.4	11.9
Jun	-	46		30	16	11	20	17	20	166	20.8	12.4
Jul	39	-	-	10	19	13	20	20		121	20.2	10.1
Aug	21	-	-	10	20	19	17	13		100	16.7	4.3
Sep	-	-	-	-	18	-	-	22		40	20.0	2.8
Oct	-	-	-	-	12	-	-	3		15	7.5	6.4
Nov	-	-	-	17	5	-	-	0		22	7.3	8.7
Dec	-	-	-	-	0	-	-	0		0		
Total	60	232	20	168	163	129	120	178	87	1157		
Mean	30.0	38.7	6.7	21.0	14.8	16.1	15.0	14.8	14.5			
SD	12.7	5.8	2.1	9.2	6.7	3.7	6.7	10.4	5.0			

Table 3.2. Relative numerical abundance of the five most important prey types in the diet of west-coast jackass penguins during 1980–88

Prey species		Percentage relative numerical abundance
Anchovy	*E. capensis*	68.2
Maasbanker	*T. trachurus*	4.0
Red-eye	*E. whiteheadii*	1.0
Pilchard	*S. ocellatus*	0.6
Cephalopods		4.3
TOTAL		78.1

Table 3.3. Annual relative numerical abundance of the five most important prey types in the diet of west-coast jackass penguins during 1980–88

Prey species	Annual relative numerical abundance (%)								
	1980	1981	1982	1983	1984	1985	1986	1987	1988
Anchovy	74.0	63.4	21.5	78.3	74.8	78.0	93.3	92.8	93.4
Maasbanker	0.2	9.8	1.3	2.4	3.0	4.3	0.6	2.0	0.0
Red-eye	*	*	1.3	3.0	0.7	1.9	0.7	0.9	1.1
Pilchard	0.0	0.3	0.2	1.3	0.1	0.6	0.0	2.1	0.7
Cephalopods	2.7	5.8	0.0	7.0	4.3	3.2	3.5	2.1	4.6
Other	23.1	20.7	75.7	8.0	17.1	12.0	1.9	0.1	0.2
total no. of prey items	553	4201	1036	2463	2826	2314	2677	1972	985
no. of months sampled	2	6	2	8	10	8	8	10	6

* no data

Table 3.4. Correspondence analysis of the monthly prey species composition of west-coast jackass penguins during 1983-88 (excluding anchovy), showing the co-ordinates and the relative and absolute contributions to the total inertia of each of the prey species on the first two principal axes

				Axis 1			Axis 2		
Prey species	Mass	Quality	Inertia	Coord	Rel	Abs	Coord	Rel	Abs
Pilchard	0.061	0.470	0.136	-0.466	0.097	0.050	0.915	0.373	0.260
Maasbanker	0.193	0.988	0.178	-0.672	0.488	0.331	-0.681	0.500	0.458
Red-eye	0.187	0.716	0.143	-0.508	0.339	0.184	0.536	0.377	0.276
Cephalopods	0.559	1.000	0.116	0.453	0.990	0.435	-0.044	0.010	0.006

Table 3.5. Correspondence analysis of the annual prey species composition of west-coast jackass penguins during February and August between 1983–88 (excluding anchovy and cephalopods), showing the co-ordinates and the relative and absolute contributions to the total inertia of each of the years on the two principal axes

				Axis 1			Axis 2		
Year	Mass	Quality	Inertia	Coord	Rel	Abs	Coord	Rel	Abs
1983	0.266	1.000	0.061	0.349	0.533	0.090	–0.327	0.467	0.336
1984	0.203	1.000	0.071	–0.530	0.800	0.159	0.265	0.200	0.169
1985	0.304	1.000	0.059	–0.432	0.956	0.158	0.093	0.044	0.031
1986	0.089	1.000	0.027	–0.251	0.205	0.016	–0.494	0.795	0.259
1987	0.138	1.000	0.224	1.225	0.922	0.577	0.355	0.078	0.206

Table 3.6. Correspondence analysis of the annual west-coast purse-seine fishery CPUE of pilchard, maasbanker and red-eye during February and August between 1983-88, showing the co-ordinates and the relative and absolute contributions to the total inertia of each of the years on the two principal axes

				Axis 1			Axis 2		
Year	Mass	Quality	Inertia	Coord	Rel	Abs	Coord	Rel	Abs
1983	0.381	1.000	0.003	0.037	0.149	0.023	0.088	0.851	0.446
1984	0.084	1.000	0.008	-0.291	0.842	0.316	-0.126	0.158	0.204
1985	0.173	1.000	0.000	0.023	0.883	0.004	-0.008	0.117	0.002
1986	0.204	1.000	0.005	-0.159	0.994	0.228	-0.012	0.006	0.005
1987	0.157	1.000	0.012	0.249	0.811	0.429	-0.120	0.189	0.344

Table 3.7. Correspondence analysis of the annual prey species composition of west-coast jackass penguins during February and August between 1983-87 (excluding anchovy and cephalopods), showing the co-ordinates and the relative and absolute contributions to the total inertia of each of the prey species on the two principal axes

				Axis 1			Axis 2		
Prey species	Mass	Quality	Inertia	Coord	Rel	Abs	Coord	Rel	Abs
Pilchard	0.198	1.000	0.251	1.102	0.956	0.671	0.236	0.044	0.131
Maasbanker	0.483	1.000	0.133	-0.491	0.878	0.326	0.183	0.122	0.191
Red-eye	0.319	1.000	0.058	0.060	0.020	0.003	-0.424	0.980	0.678

Table 3.8. Correspondence analysis of annual west-coast purse-seine fishery CPUE of pilchard, maasbanker and red-eye during February and August between 1983-87, showing the co-ordinates and the relative and absolute contributions to the total inertia of each of the species on the two principal axes

				Axis 1			Axis 2		
Prey species	Mass	Quality	Inertia	Coord	Rel	Abs	Coord	Rel	Abs
Pilchard	0.354	1.000	0.011	0.158	0.843	0.393	0.068	0.157	0.252
Maasbanker	0.012	1.000	0.011	0.747	0.609	0.308	−0.599	0.391	0.680
Red-eye	0.634	1.000	0.007	−0.103	0.938	0.299	−0.026	0.062	0.068

Table 3.10. Changes in the annual relative numerical abundance (%) of pelagic shoaling fish species and cephalopods in the diet of west-coast jackass penguins over a 30-year period (after Burger & Cooper 1984)

Sample period:	1954-55	1977-78	1986
Source of data:	Davies (1956)	Cooper (1984)	this study
Pilchard	49	1	0
Anchovy	44	84	93
Maasbanker	2	0	<1
Red-eye	0	14	<1
Cephalopods	3*	1	3
No. of birds examined	112	30	120

* includes other fish and crustaceans

Table 4.1. The number of monthly stomach samples collected from jackass penguins at the southwest coast (Dyer Island) during 1982–88. No diet samples were obtained in 1986, and in September and December of any year

	1982	1983	1984	1985	1986	1987	1988	Total	Mean
Jan	-	-	-	-	-	20	-	20	20.0
Feb	-	-	17	15	-	-	20	52	17.3
Mar	-	26	-	-	-	20	-	46	23.0
Apr	-	-	-	-	-	-	50	50	50.0
May	-	-	-	-	-	20	50	70	35.0
Jun	18	-	-	-	-	22	70	110	36.7
Jul	-	-	18	-	-	61		79	39.5
Aug	-	21	-	-	-	20		41	20.5
Oct	17	-	-	-	-	20		37	18.5
Nov	-	20	20	20	-	-		60	20.0
Total	35	67	55	35	-	183	190	565	
Mean	17.5	22.3	18.3	17.5	-	22.9	47.5		

Table 4.2. Relative numerical abundance of the five most important prey types in the diet of southwest-coast jackass penguins during 1982–88

Prey species		Percentage relative numerical abundance
Anchovy	*E. capensis*	95.8
Pilchard	*S. ocellatus*	1.1
Maasbanker	*T. trachurus*	0.7
Red-eye	*E. whiteheadii*	0.5
Cephalopods		0.4
TOTAL		98.5

Table 4.3. Annual relative numerical abundance of pelagic shoaling fish and cephalopods in the diet of southwest-coast jackass penguins during 1982-88

Prey species	Annual relative numerical abundance (%)						
	1982	1983	1984	1985	1986	1987	1988
Anchovy	97.2	96.3	81.0	98.9	-	98.3	96.5
Pilchard	0.7	0.3	3.6	0.0	-	0.4	1.6
Maasbanker	0.5	1.4	4.1	0.0	-	0.2	0.2
Red-eye	0.0	0.3	0.1	0.0	-	0.6	0.6
Cephalopods	1.3	1.0	0.1	1.1	-	0.2	0.6
Other	0.3	0.7	11.1	0.0	-	0.3	0.5
total no. of prey items	395	706	921	181	-	4017	3379
no. of months sampled	2	3	3	1	-	7	4

Table 4.4. Correspondence analysis of the prey species (excluding anchovy) in the diet of jackass penguins at the west- and southwest coast during 1982–88, showing the co-ordinates and the relative and absolute contributions to the total inertia of each of the prey species on all three principal axes

				Axis 1			Axis 2			Axis 3		
Prey species	Mass	Quality	Inertia	Coord	Rel	Abs	Coord	Rel	Abs	Coord	Rel	Abs
Pilchard	0.110	0.821*	0.311	1.298	0.708	0.520	0.519	0.113	0.093	0.653	0.179	0.277
Maasbanker	0.236	0.987*	0.284	0.051	0.003	0.002	−0.998	0.984	0.743	0.116	0.013	0.019
Red−eye	0.188	0.297*	0.192	0.476	0.263	0.120	0.169	0.033	0.017	−0.777	0.703	0.675
Cephalopods	0.466	0.973*	0.213	−0.524	0.714	0.359	0.316	0.259	0.147	0.101	0.027	0.028

* in two dimensions (1.000 in all three)

Table 4.5. Anchovy < 60 mm as a proportion (%) of all anchovy collected from monthly diet samples of jackass penguins at the west and southwest coast between 1983–88

Year	Month	Prop. of anchovy < 60 mm (%)	
		West coast	Southwest coast
1983	Mar	0.4	0.0
	Aug	8.2	0.6
	Nov	1.9	0.0
1984	Feb	4.7	22.2
	Jul	7.5	11.0
	Nov	0.0	0.0
1985	Feb	9.3	0.0
1987	Jan	27.1	2.3
	Mar	3.5	0.0
	May	26.4	0.4
	Jun	2.4	0.0
	Jul	43.1	0.0
	Aug	42.0	9.2
	Oct	13.6	6.6
1988	Feb	0.7	0.0
	Apr	27.2	0.3
	May	52.7	1.9
	Jun	41.3	0.5

Table 4.6. Statistical comparisons of inter–annual monthly size–frequency distributions and median lengths of anchovy in the diet of southwest–coast jackass penguins during 1982–88, using Conover's (1971) chi-square test for differences in probabilities and the multisample median test of Mood (1950). No diet samples were obtained in 1986, and in September and December of any year

Month	n	Years sampled	Size–frequency distribution			Median length		
			df	*T*	Sign. level	df	X^2	Sign. level
Feb	3	1984–5/7	6	114	$P < 0.0001$	2	58	$P < 0.0001$
Mar	2	1983/7	3	234	$P < 0.0001$	1	81	$P < 0.0001$
May	2	1987–8	7	618	$P < 0.0001$	1	497	$P < 0.0001$
Jun	3	1982/7–8	6	2384	$P < 0.0001$	2	226	$P < 0.0001$
Jul	2	1984/7	8	1140	$P < 0.0001$	1	144	$P < 0.0001$
Aug	2	1983/7	7	311	$P < 0.0001$	1	266	$P < 0.0001$
Oct	2	1982/7	7	219	$P < 0.0001$	1	38	$P < 0.0001$
Nov	3	1983–5	16	200	$P < 0.0001$	2	87	$P < 0.0001$

Table 4.7. Statistical comparison of monthly median caudal length (in mm) of anchovy taken by jackass penguins at the west and southwest coast during 1983–88, using the median test of Mood (1950). For all tests df = 1 (see text). The ≥ 95 % confidence interval range is given in brackets

Year	Month	Median caudal length (mm)		χ^2
		W coast	SW coast	
1983	Mar	100.9 (99.3–102.3)	103.8 (98.0–104.9)	1.1 +
	Aug	78.2 (77.0–79.5)	86.8 (85.8–87.8)	80.7 ***
	Nov	79.8 (76.7–82.9)	96.4 (95.0–99.0)	113.0 ***
1984	Feb	85.9 (78.0–91.9)	97.4 (92.2–103.3)	9.8 **
	Jul	78.8 (76.3–81.6)	93.2 (91.9–95.5)	93.1 ***
	Nov	78.0 (70.5–83.0)	85.4 (81.9–89.1)	7.1 **
1985	Feb	80.5 (68.8–88.0)	108.0 (100.5–115.5)	17.1 ***
1987	Jan	63.8 (62.7–65.1)	77.1 (75.7–78.8)	88.8 ***
	Mar	76.2 (74.3–77.9)	76.5 (75.9–77.6)	0.1 +
	May	67.7 (65.2–70.8)	75.3 (74.7–76.0)	33.5 ***
	Jun	80.8 (77.4–82.8)	76.8 (76.3–77.3)	7.5 **
	Jul	62.1 (60.7–63.6)	77.0 (76.7–77.3)	120.6 ***
	Aug	62.5 (60.7–64.3)	75.7 (74.7–76.6)	101.6 ***
	Oct	73.0 (64.6–80.5)	67.7 (66.9–68.5)	1.6 +
1988	Feb	82.8 (80.7–85.1)	79.8 (77.7–80.9)	7.7 **
	Apr	67.8 (63.7–72.5)	78.0 (77.6–78.4)	28.2 ***
	May	60.1 (58.9–61.5)	85.4 (84.7–86.1)	227.5 ***
	Jun	66.2 (62.8–69.7)	79.1 (78.7–79.6)	6.3 *

+ not significant
* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

Table 4.8. Relative numerical abundance (%) of the most important pelagic prey species of jackass penguins at localities along the South African coast. East-coast data were obtained from Randall & Randall (1986)

Sample period:	1980–88	1982–88	1979–81
Locality:	West coast	Southwest Coast	East Coast
Anchovy	68.2	95.8	32.1
Pilchard	0.6	1.1	5.2
Maasbanker	4.0	0.7	0.4*
Red-eye	1.0	0.5	54.3
Cephalopods	4.3	0.4	0.7

* *Trachurus capensis*

Table 5.1. Estimates of anchovy recruit biomass from acoustic surveys during 1985 - 1988 in strata corresponding to the coastal area off Saldanha Bay, and the proportion of small (< 56 mm) anchovy in the diet of west-coast jackass penguins in the same month(s) as the survey

Year	Stratum	Recruit biomass (1 000 t)		Small anchovy (% by number)	Source
		Inshore	Offshore		
May/June 1985	D	50	175	2.8	Hampton (1987)
June 1986	D	53	4	3.7	Hampton (1987)
July 1987	C	31	279	21.5	SFRI*
July 1988	C	5	102	20.9	SFRI*

* M.J. Armstrong (unpubl. data)

Table 5.2. Annual maximum percentage (by number), and the month in which it occurred, of anchovy < 56 mm caudal length in the diet of west-coast jackass penguins during 1981–88. The total number of anchovy measured in the relevant months is given

Year	%	Month	Tot. no.
1981	21.3	Feb	127
1982	-	-	-
1983	24.9	May	366
1984	48.7	Mar	78
1985	62.9	Apr	462
1986	41.4	Apr	389
1987	41.8	Apr	170
1988	37.5	Jun	397

Table 5.3. Coefficients of simple linear correlation between acoustic recruitment estimates and the proportion of anchovy < 56 mm in caudal length in the diet of west-coast jackass penguins, integrated over different annual periods during 1985–88

Annual period	r	df	Sign. level
Jan	−0.6093	2	ns +
Jan – Feb	−0.4776	2	ns +
Jan – Mar	−0.0937	2	ns +
Jan – Apr	−0.6602	2	ns +
Jan – May	−0.5513	2	ns +
Jan – Jun	−0.7283	2	ns +

+ not significant (P > 0.05)

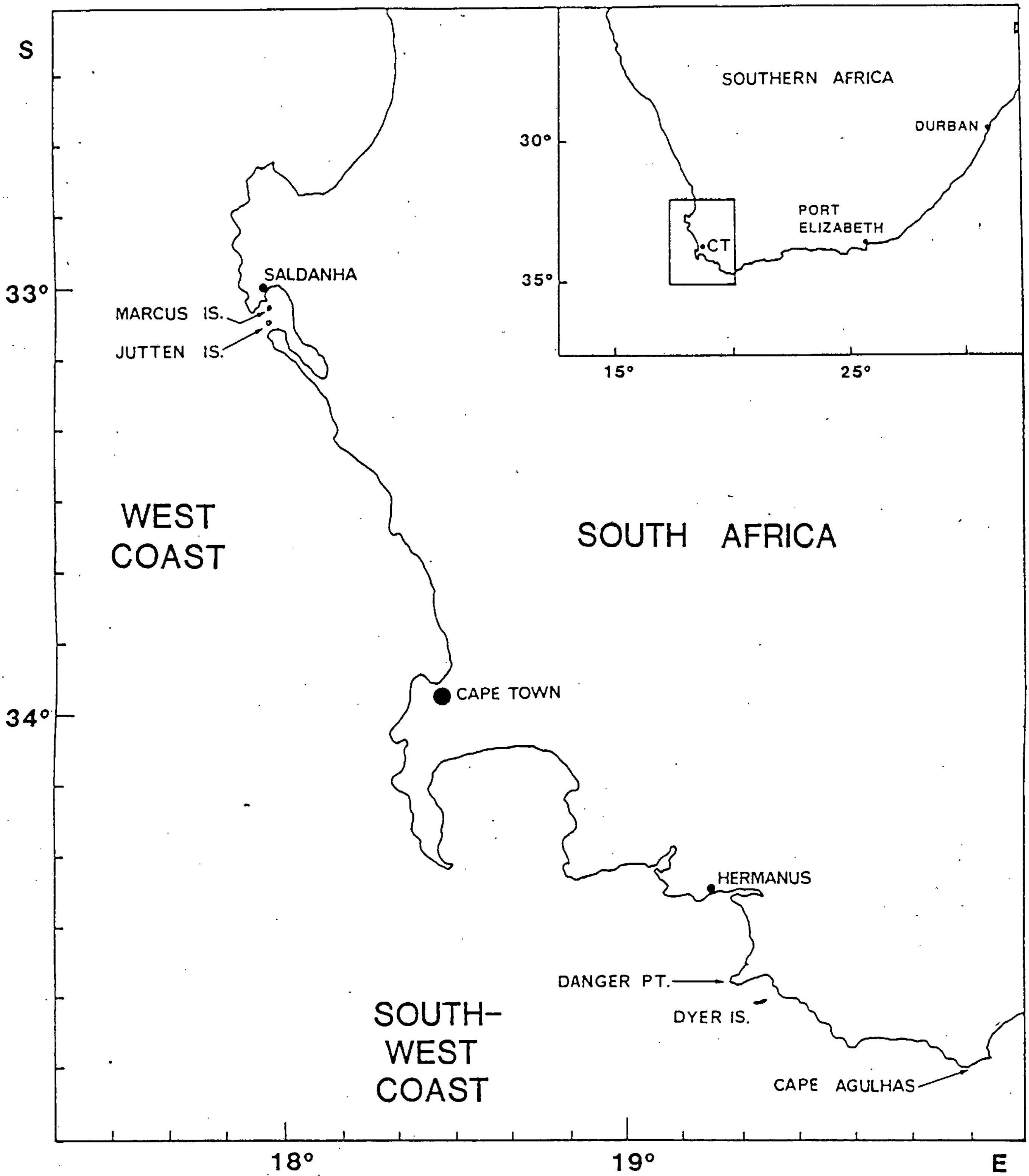

Figure 1.1. A map of the study sites at the west and southwest coast of South Africa, showing the position of Marcus, Jutten and Dyer Islands.

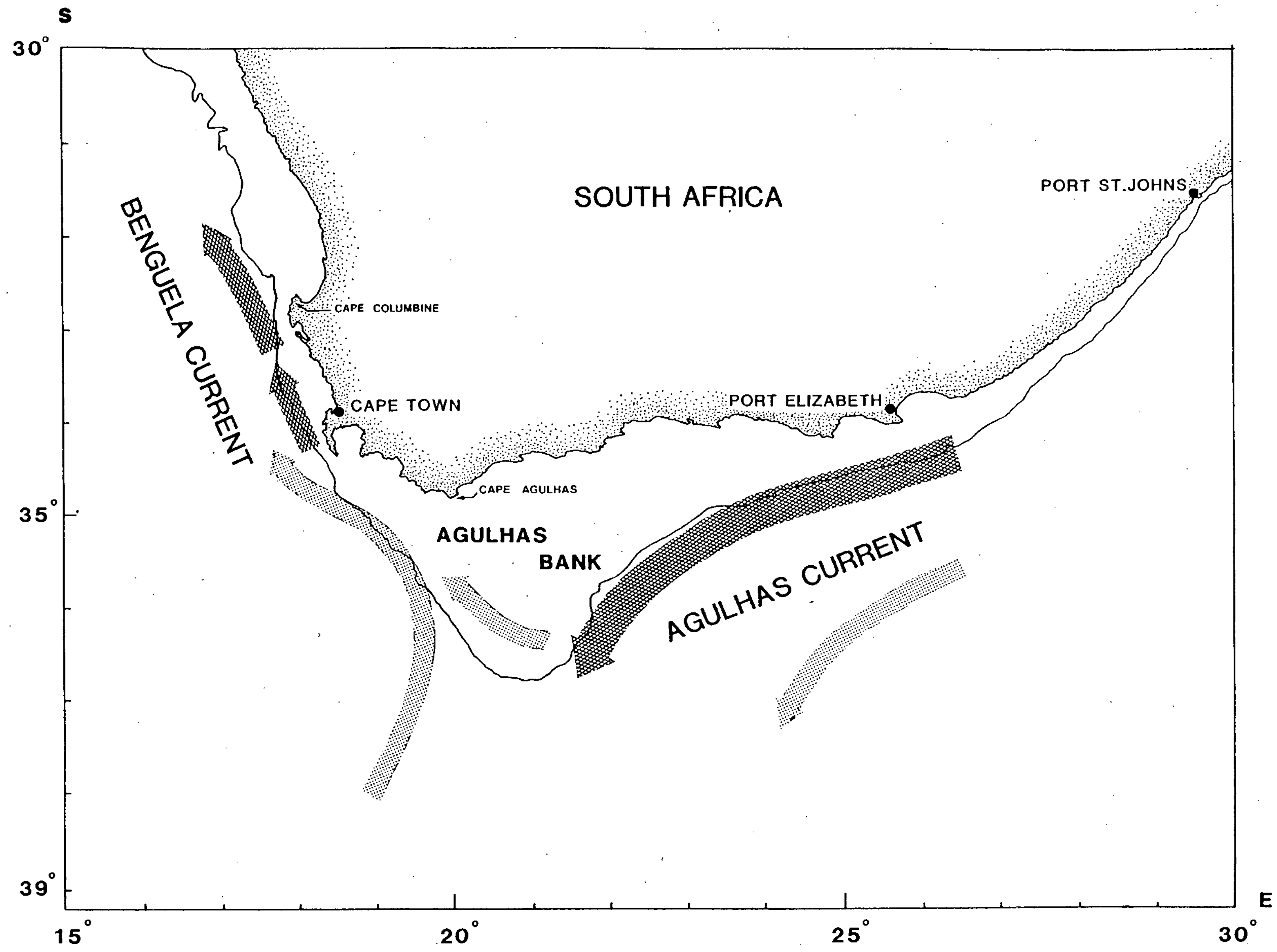

Figure 1.2. A map of southern Africa, showing current systems and the 200-m isobath (after Boyd *et al*. 1985).

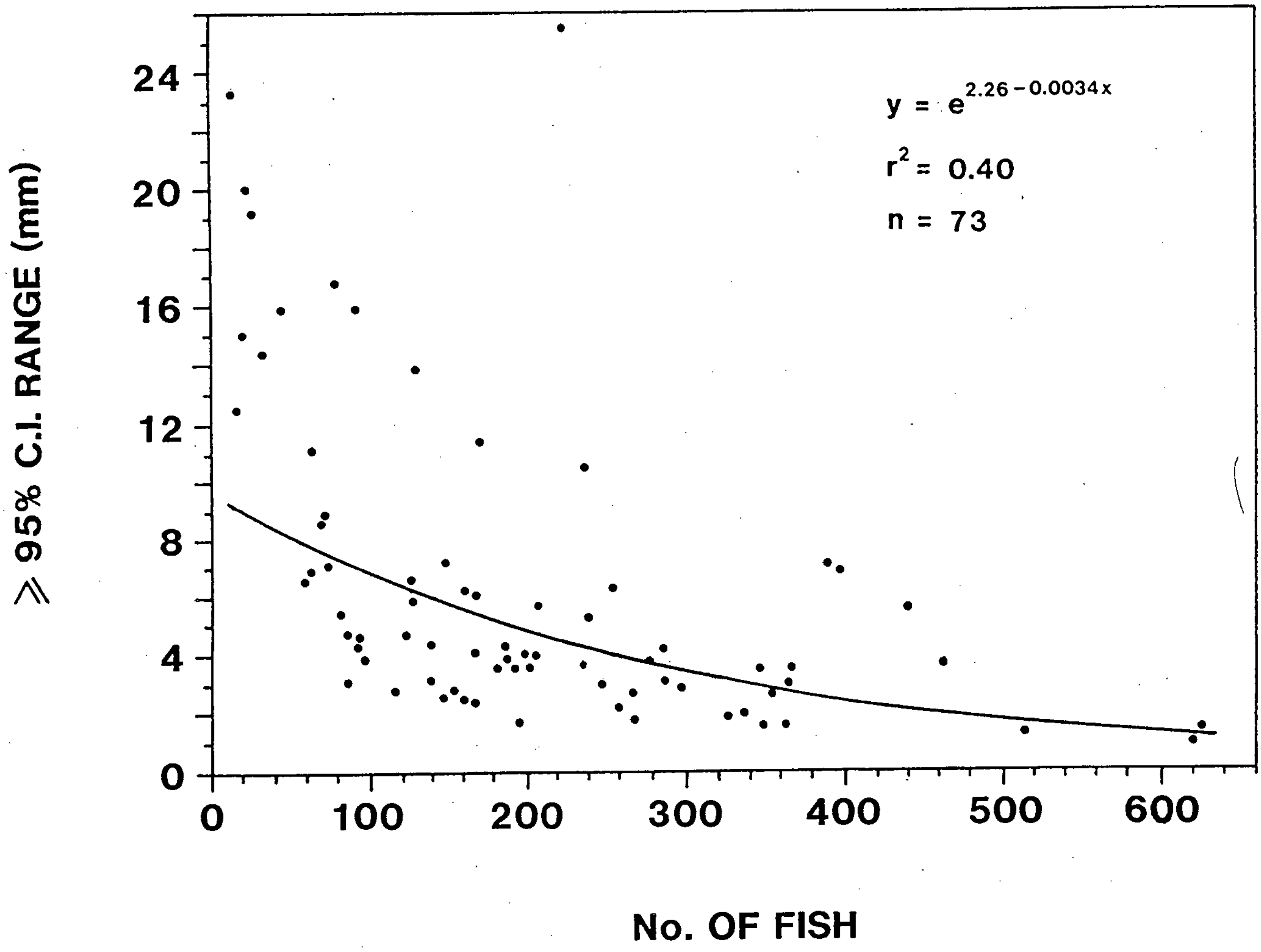

Figure 2.1. Exponential regression of the range of the ≥ 95 % confidence interval of median anchovy length on the number of fish measured ($P < 0.00001$).

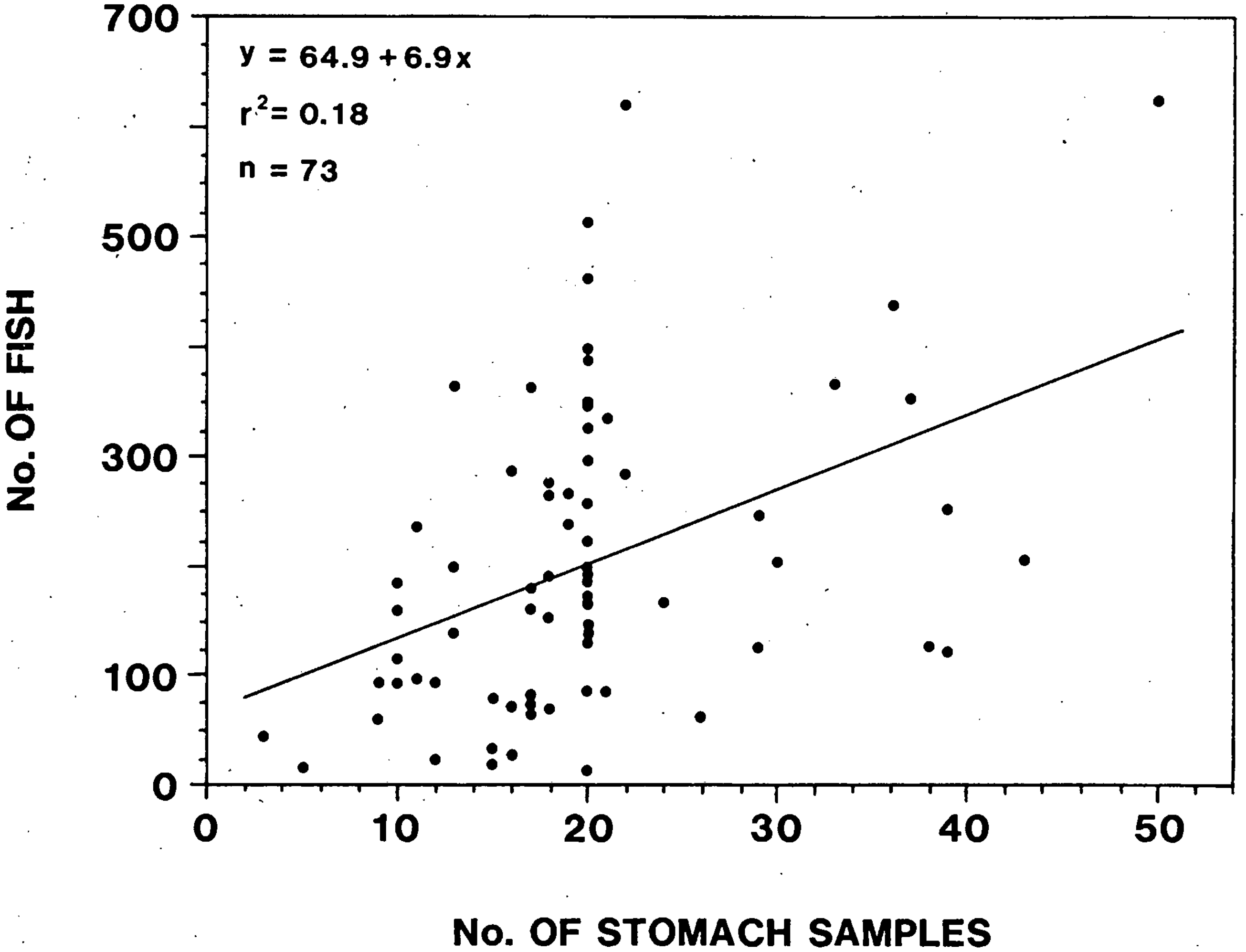

Figure 2.2. Simple linear regression of the number of anchovy measured on the number of jackass penguin stomach samples obtained ($P < 0.0005$).

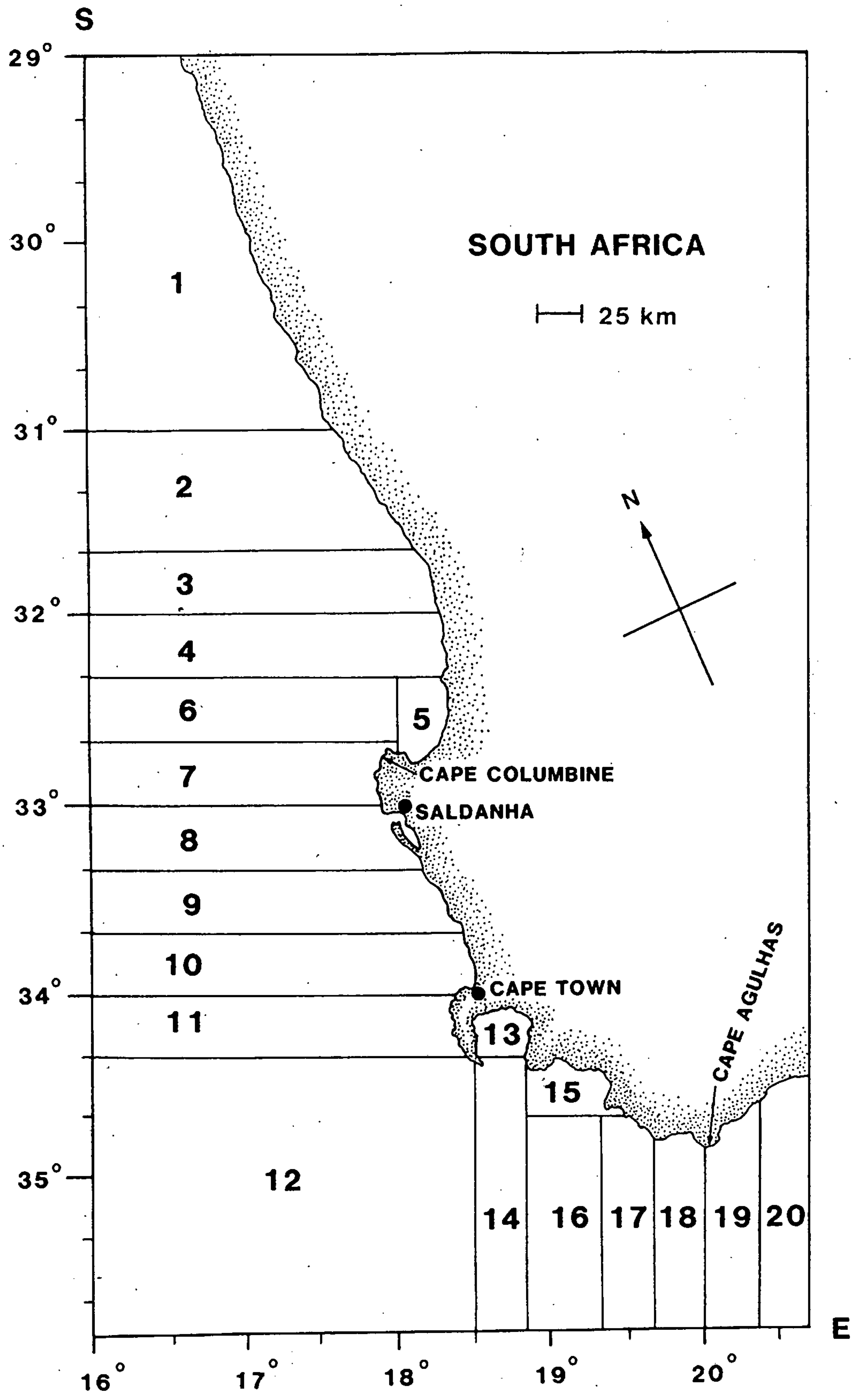

Figure 3.1. A map showing all South African purse-seine fishery pool areas (after Sea Fisheries Research Institute). Pool areas 1-12 and 13-20 constitute the west and southwest coast, respectively.

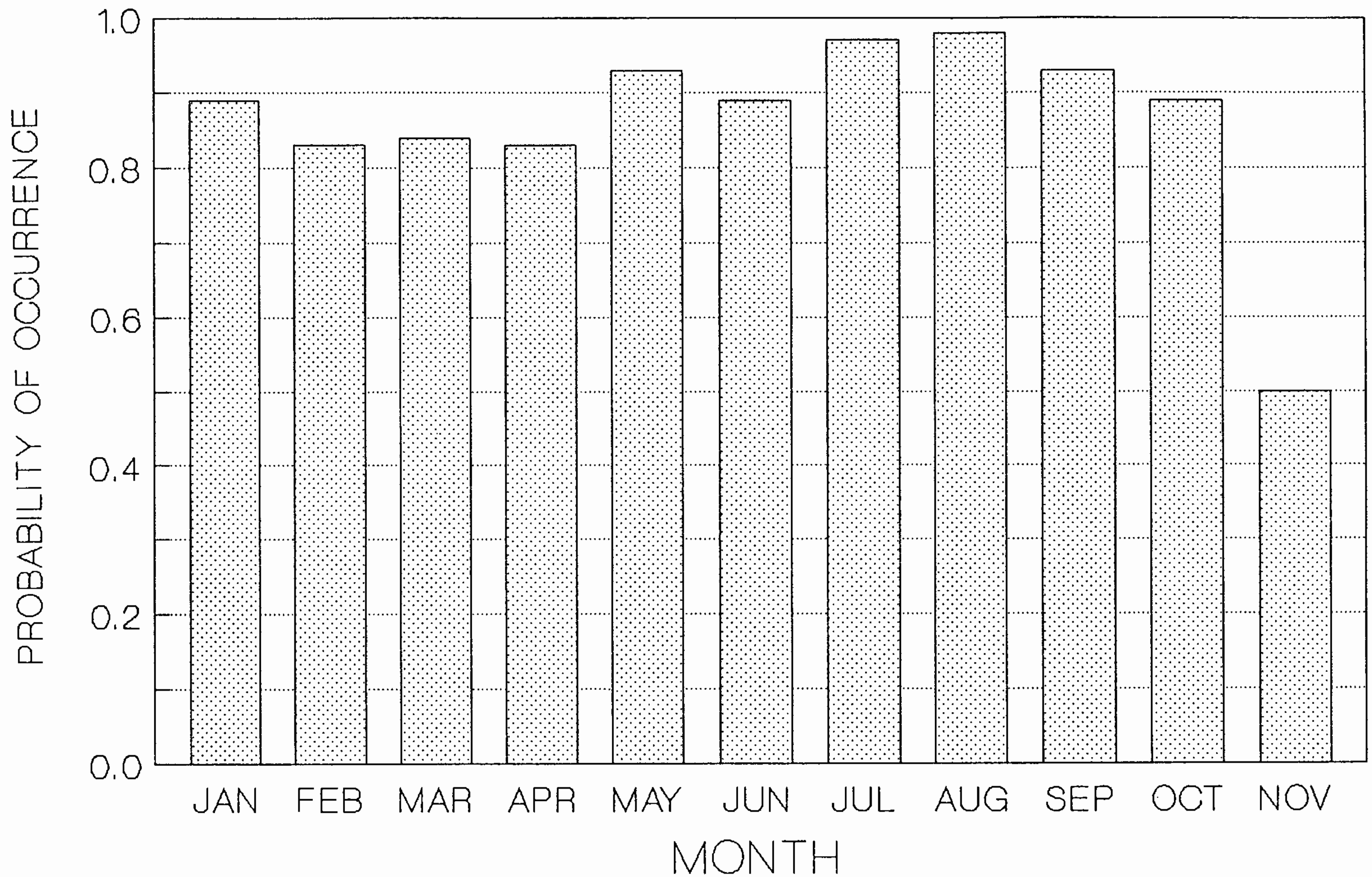

Figure 3.2. Monthly probability of occurrence of anchovy in west-coast jackass penguin diet during 1980–88.

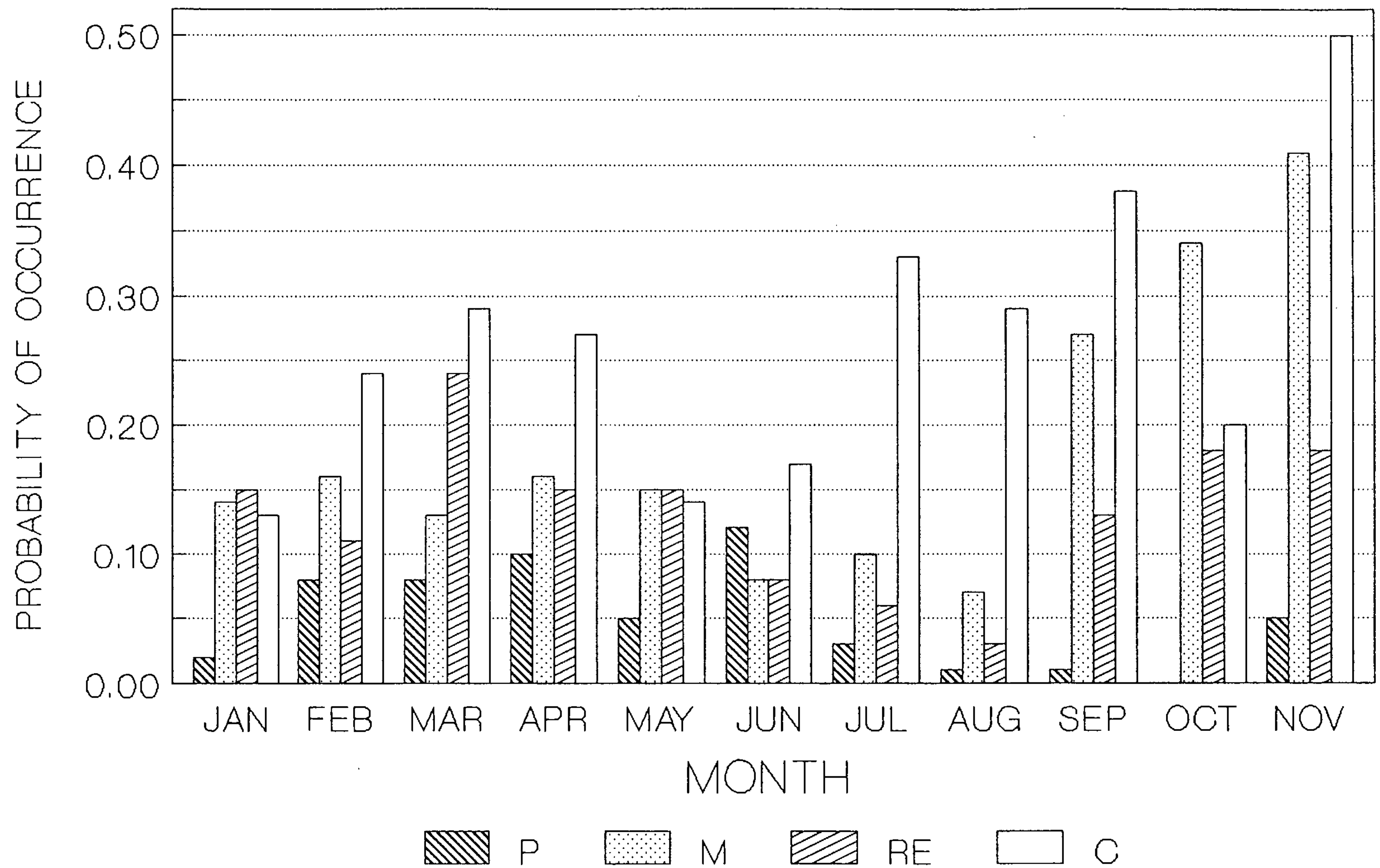

Figure 3.3. Monthly probability of occurrence of pilchard (P), maasbanker (M), red-eye (RE) and cephalopods (C) in west-coast jackass penguin diet during 1980–88.

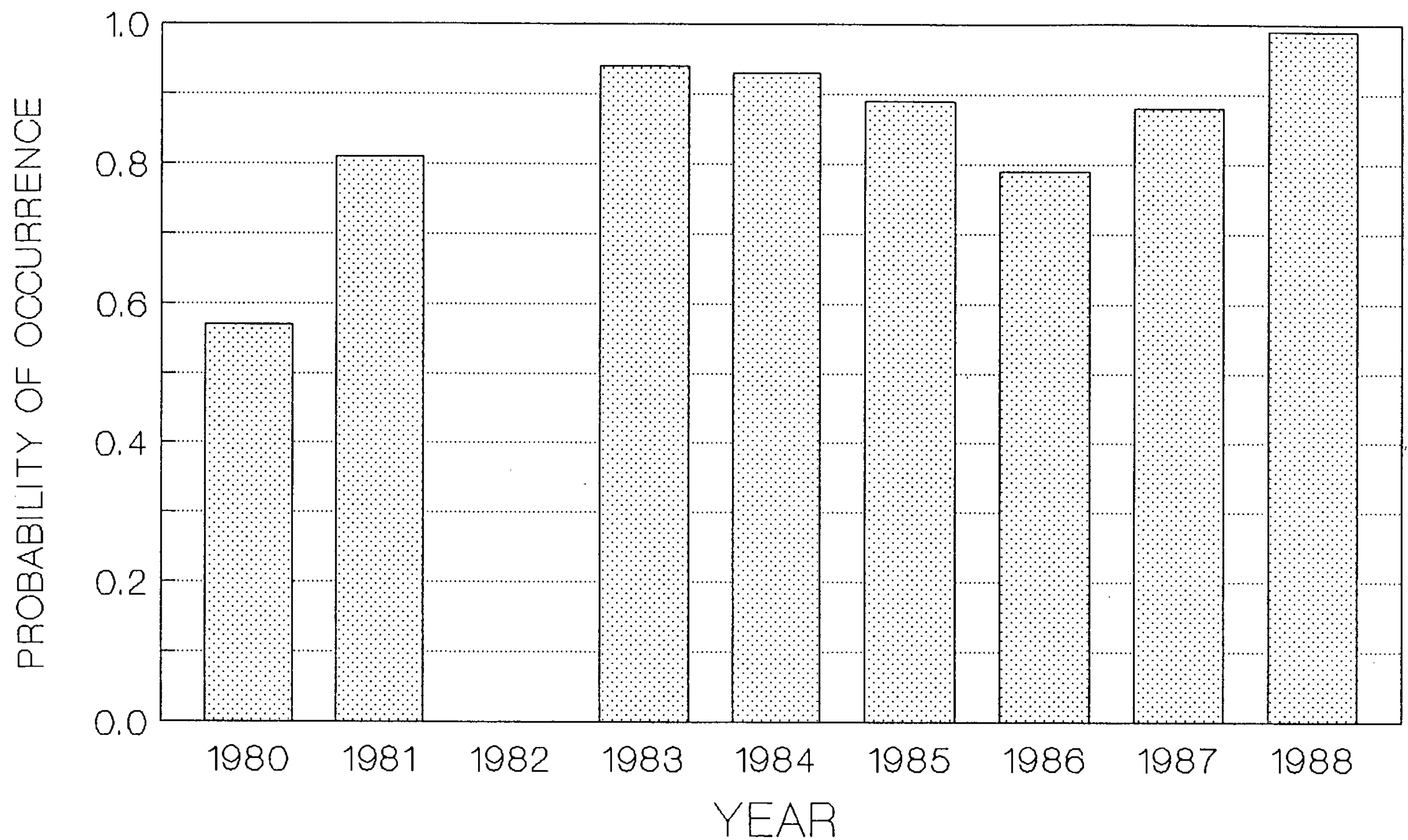

Figure 3.4. Annual probability of occurrence of anchovy in west-coast jackass penguin diet during 1980–88. Data for 1982 were excluded (see text).

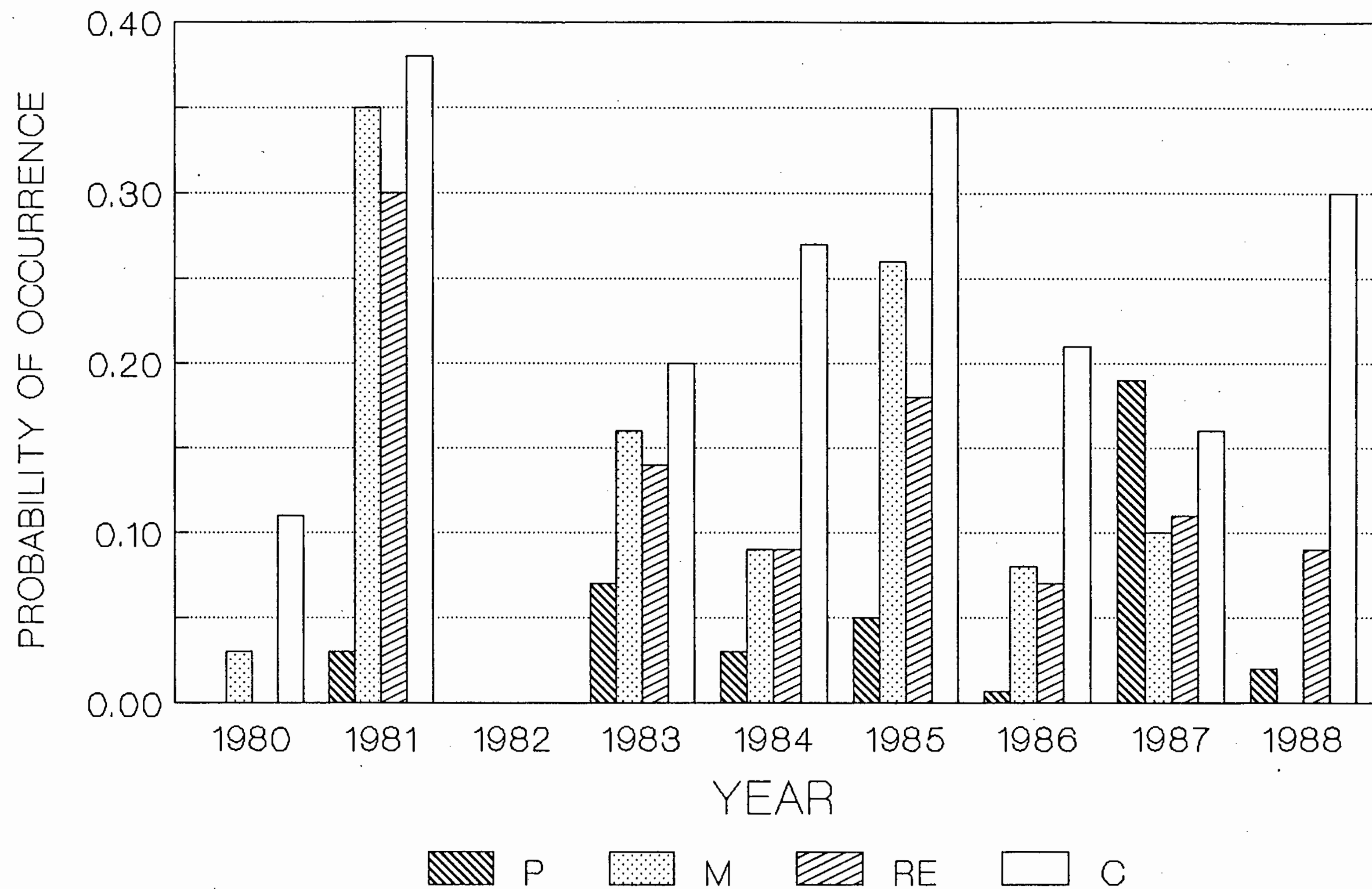

Figure 3.5. Annual probability of occurrence of pilchard (P), maasbanker (M), red-eye (RE) and cephalopods (C) in west-coast jackass penguin diet during 1980–88. Data for 1982 were excluded (see text).

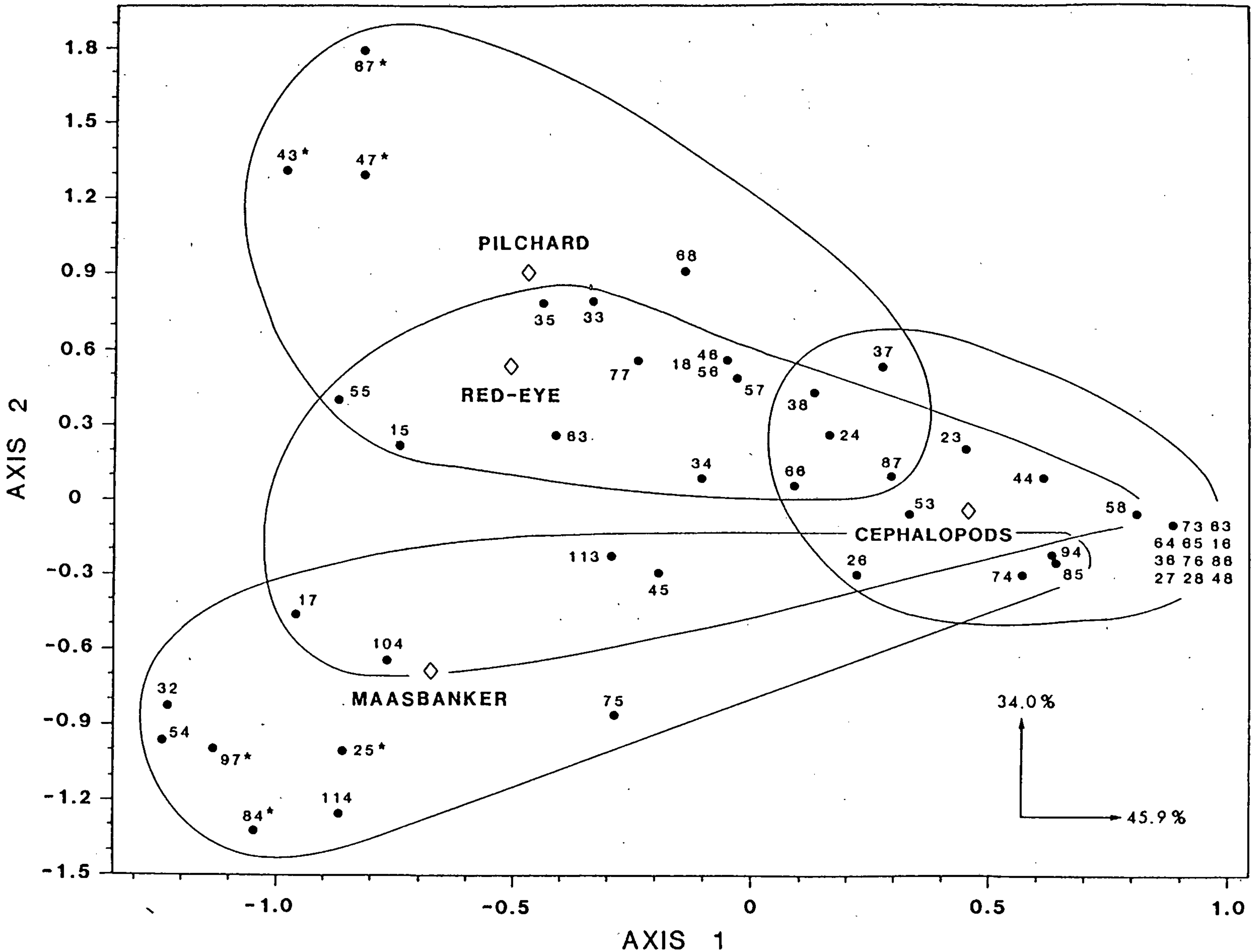

Figure 3.6. A correspondence analysis plot showing the monthly prey species composition of the diet of west-coast jackass penguins during 51 months between 1983–88. The first and second/third digit indicate(s) the month and year, respectively. Asterisks indicate supplementary points. Anchovy was treated as a supplementary point (see text) and is coincident with August 1987. In order to be able to judge the relative closeness of the points correctly, the scale of the horizontal and vertical axes is proportional to the square root of the first and second principal inertias, respectively (Moran & Gornbein 1988).

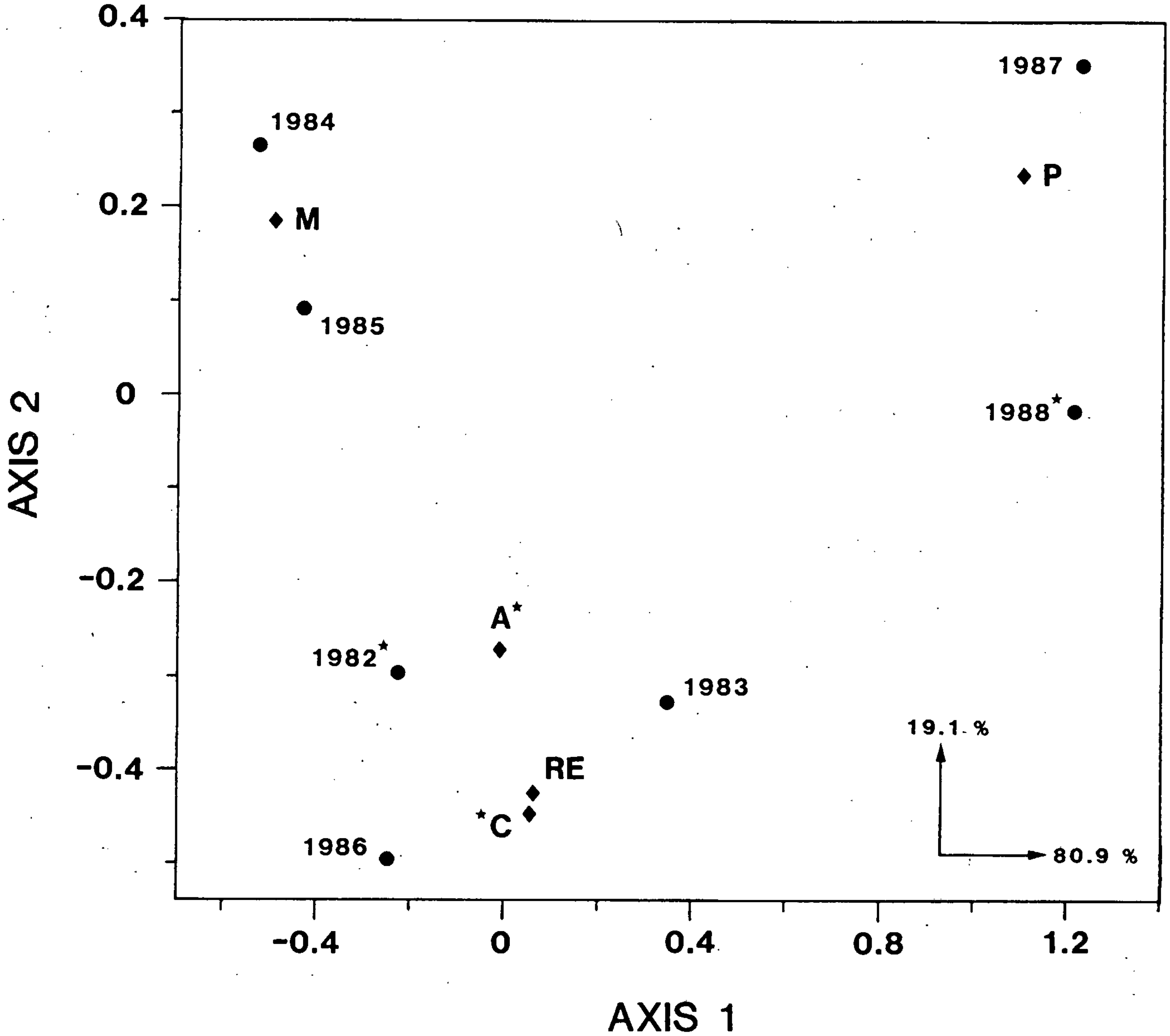

Figure 3.7. A correspondence analysis plot showing the annual prey species composition of the diet of west-coast jackass penguins during 1983-87 (February to August). Asterisks indicate supplementary points (see text).

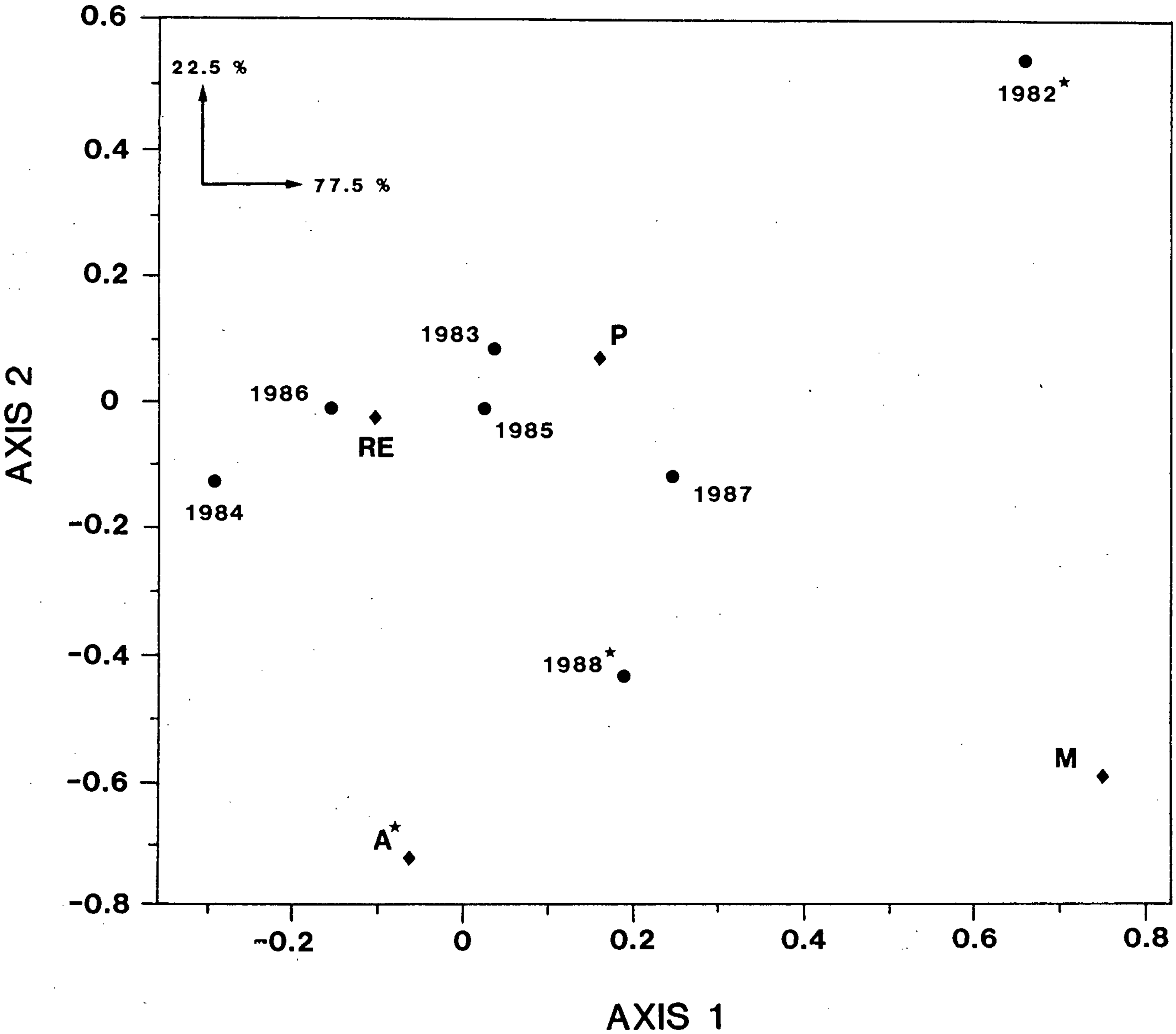

Figure 3.8. A correspondence analysis plot showing the catch-per-unit-effort (CPUE) for different species of west-coast purse-seine catches (fishing pool areas 1-12) during 1983-87 (February to August). Asterisks indicate supplementary points (see text).

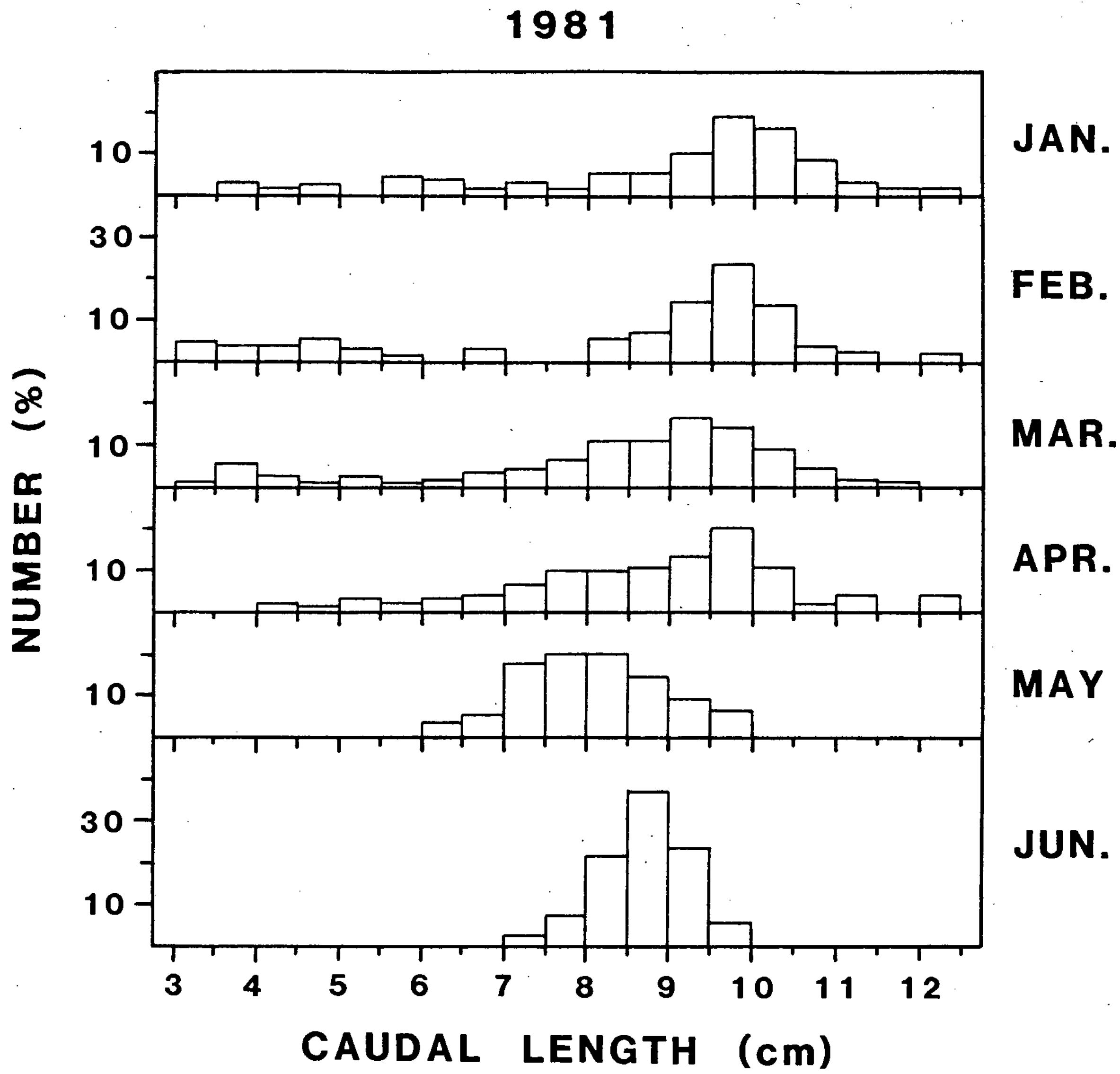

Figure 3.9. Monthly size-frequency distribution of anchovy in west-coast jackass penguin diet during 1981. No diet samples were obtained after June.

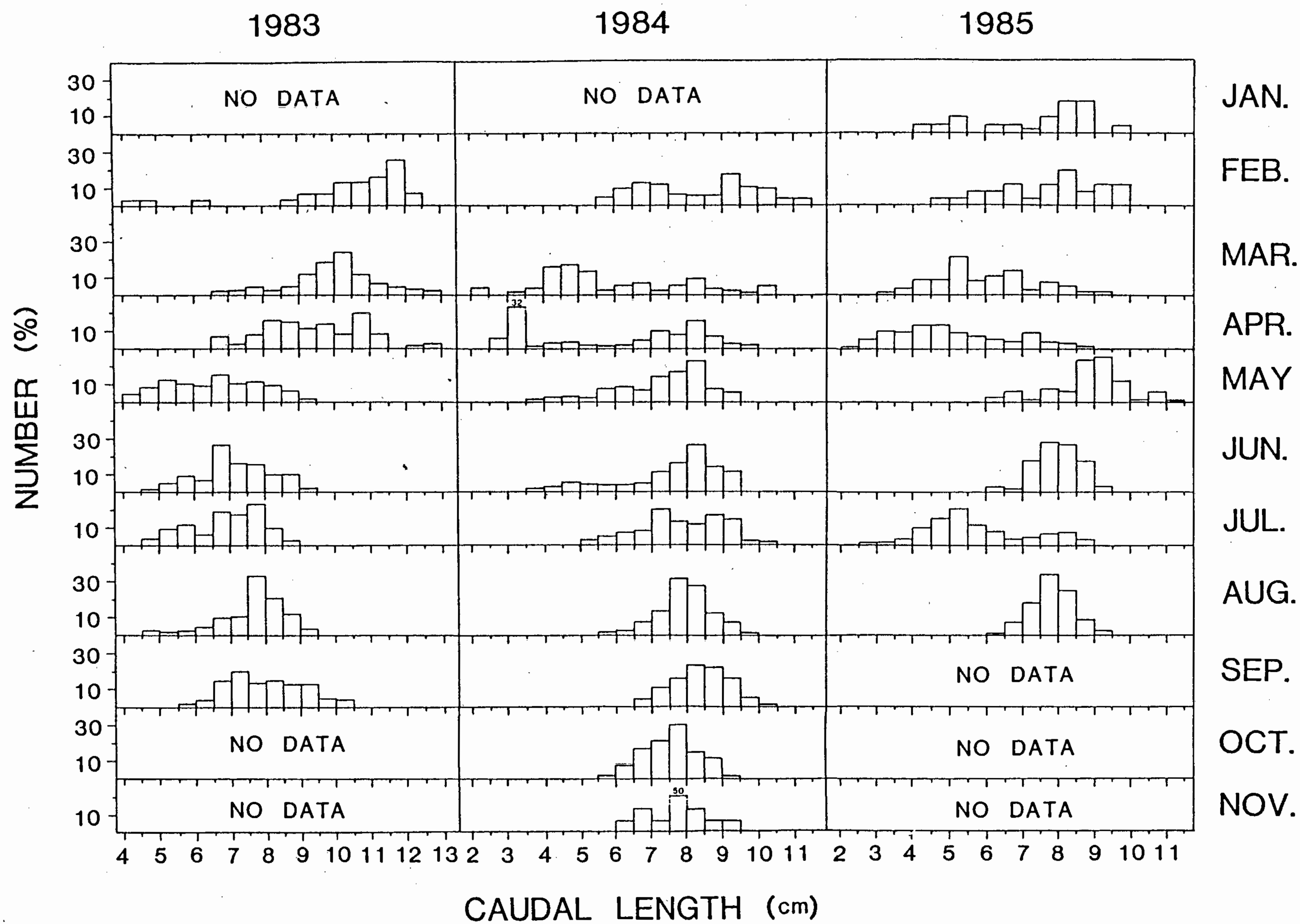

Figure 3.10. Monthly size-frequency distribution of anchovy in west-coast jackass penguin diet between 1983-85.

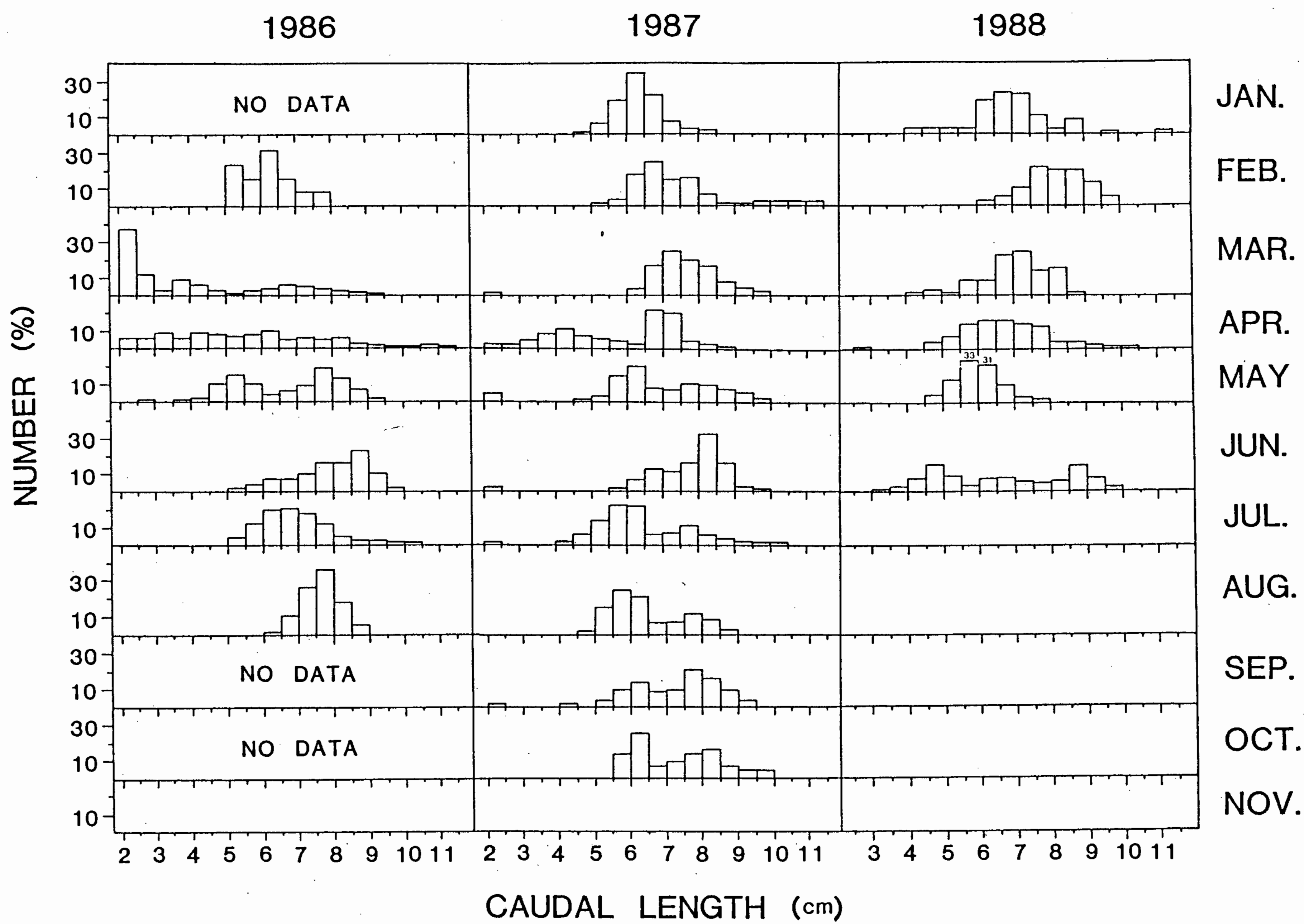

Figure 3.11. Monthly size-frequency distribution of anchovy in west-coast jackass penguin diet between 1986-88.

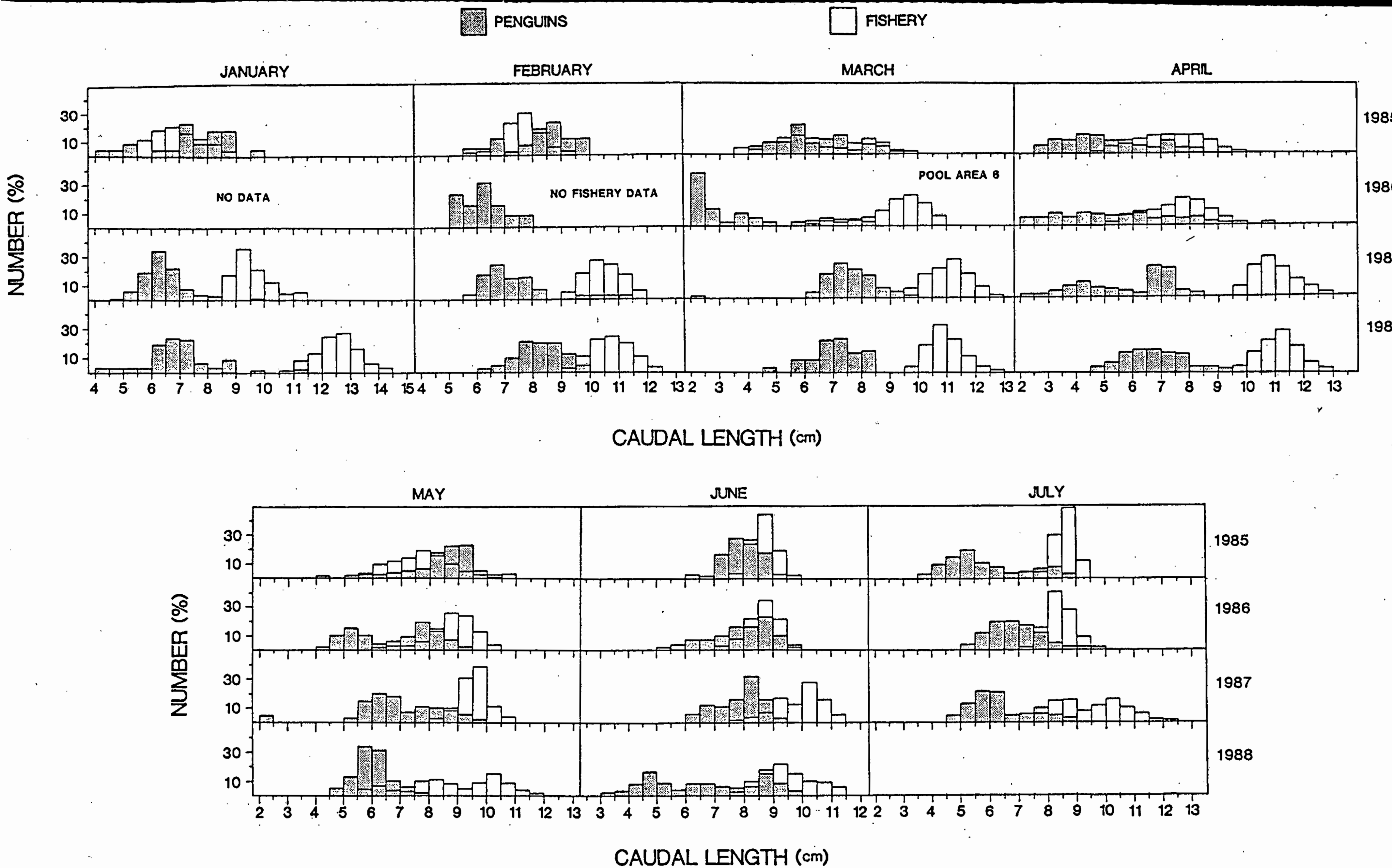

Figure 3.12. Monthly size-frequency distribution of anchovy in west-coast jackass penguin diet and purse-seine fishery catches in South African fishing pool areas seven and eight between 1985-88.

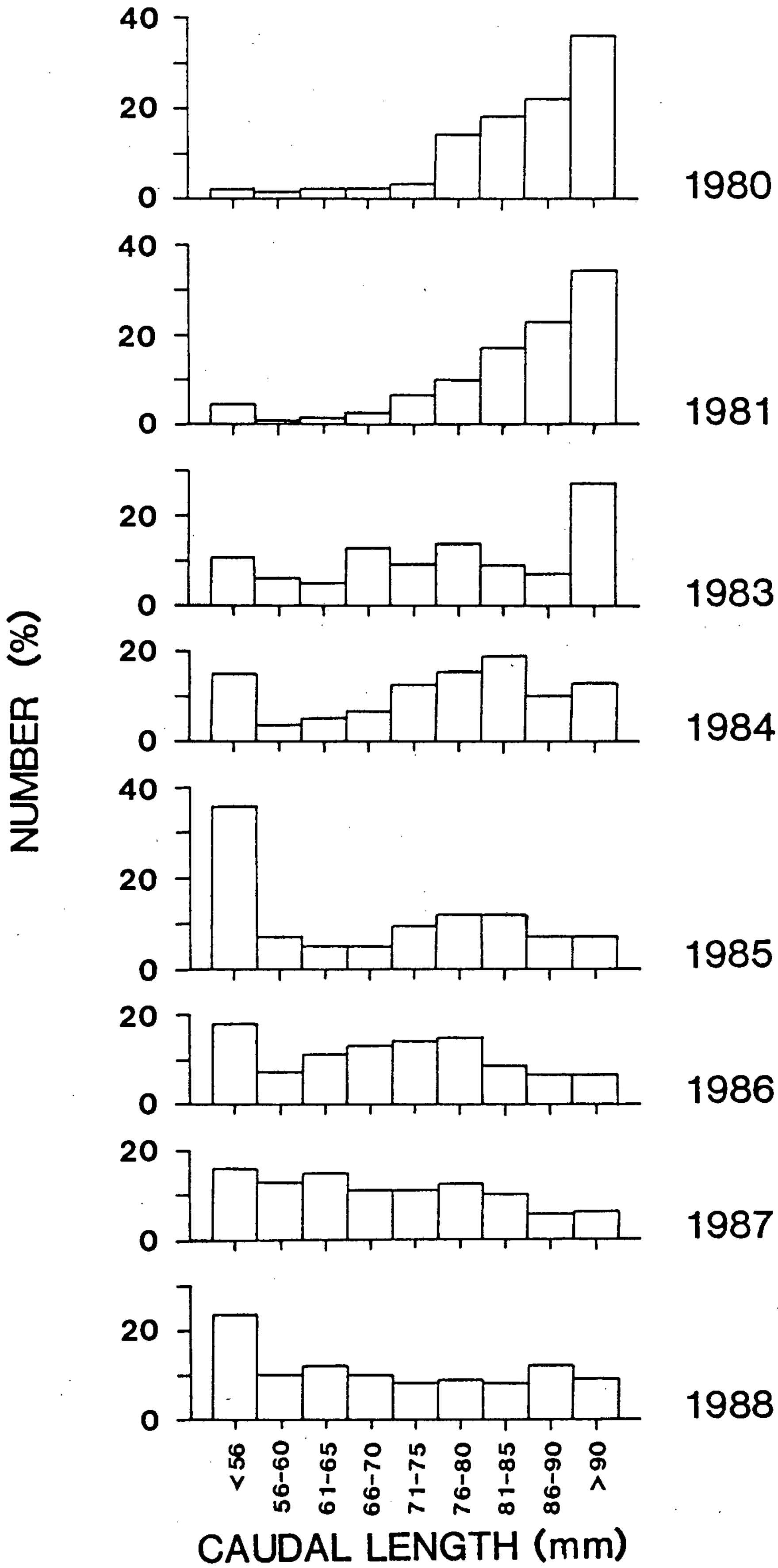

Figure 3.13. Annual size-frequency distribution of anchovy in west-coast jackass penguin diet between 1980-88. The data for 1982 were excluded (see text).

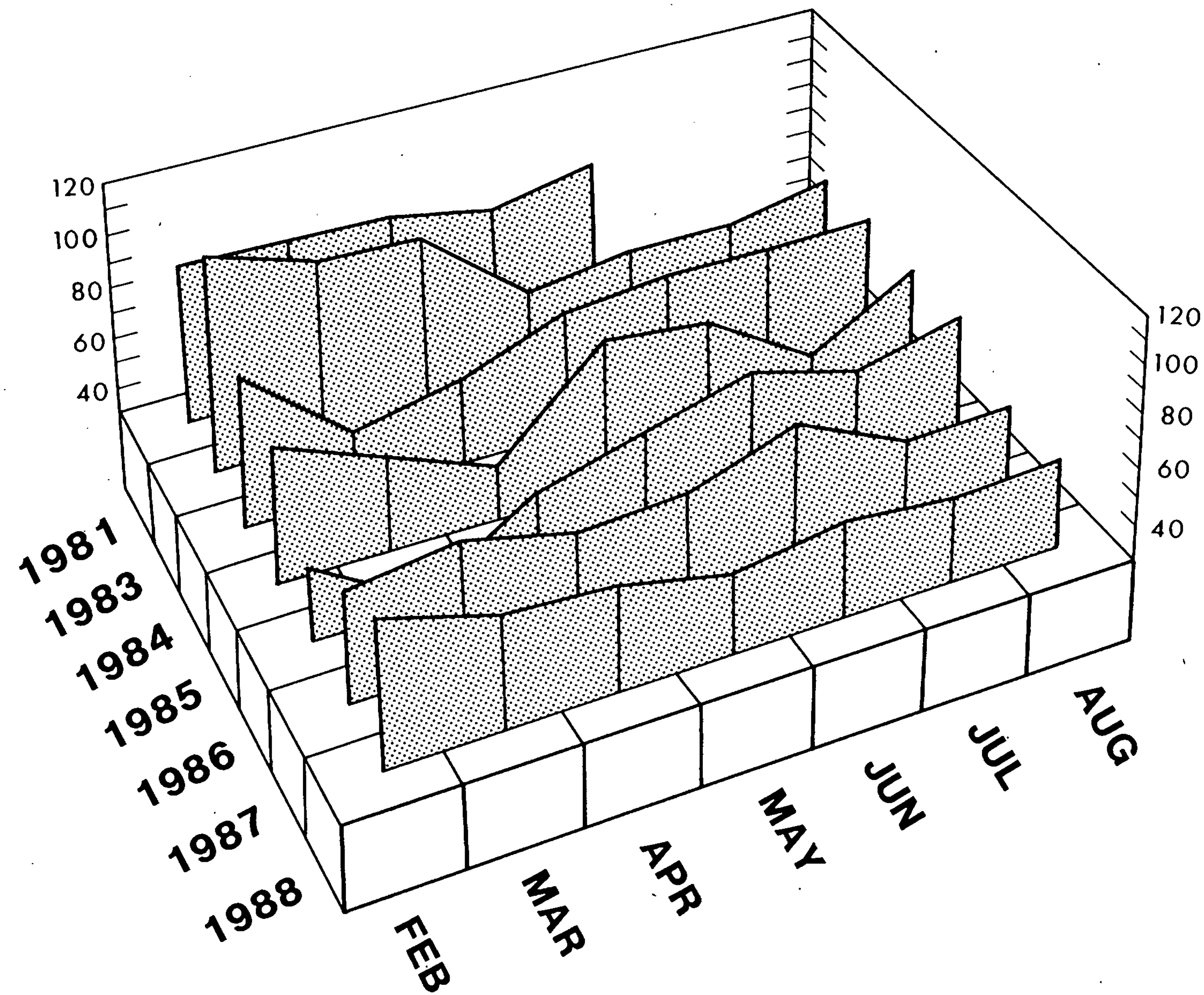

Figure 3.14. Intra-annual monthly median caudal length (in mm) of anchovy taken by west-coast jackass penguins between 1981–88.

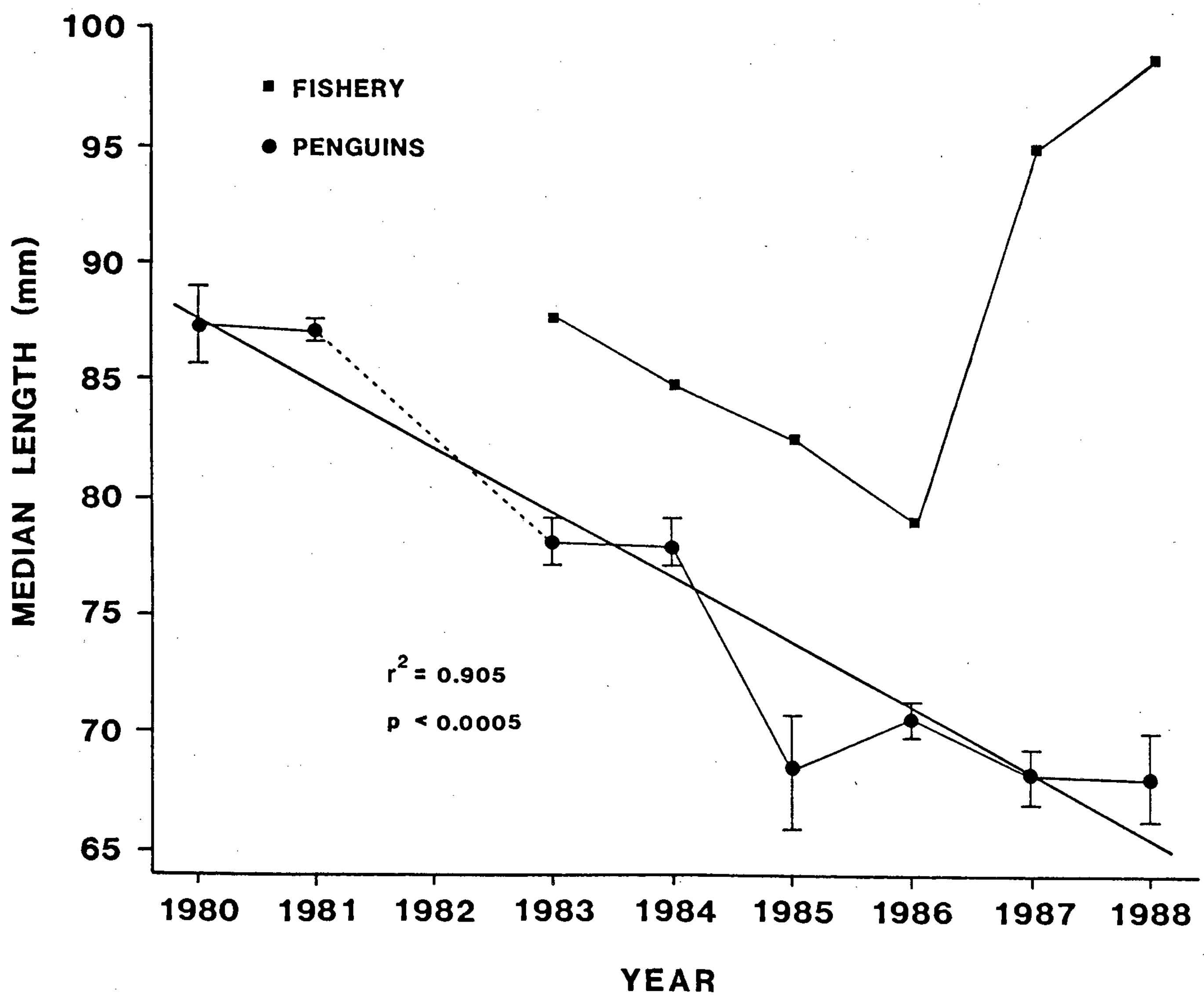

Figure 3.15. Annual median caudal length of anchovy in west-coast jackass penguin diet and total South African purse-seine fishery catches between 1980-88 and 1983-88, respectively. The simple linear regression of diet-based median length on year was significant. Vertical bars represent the $\geq$ 95 % confidence interval around median lengths.

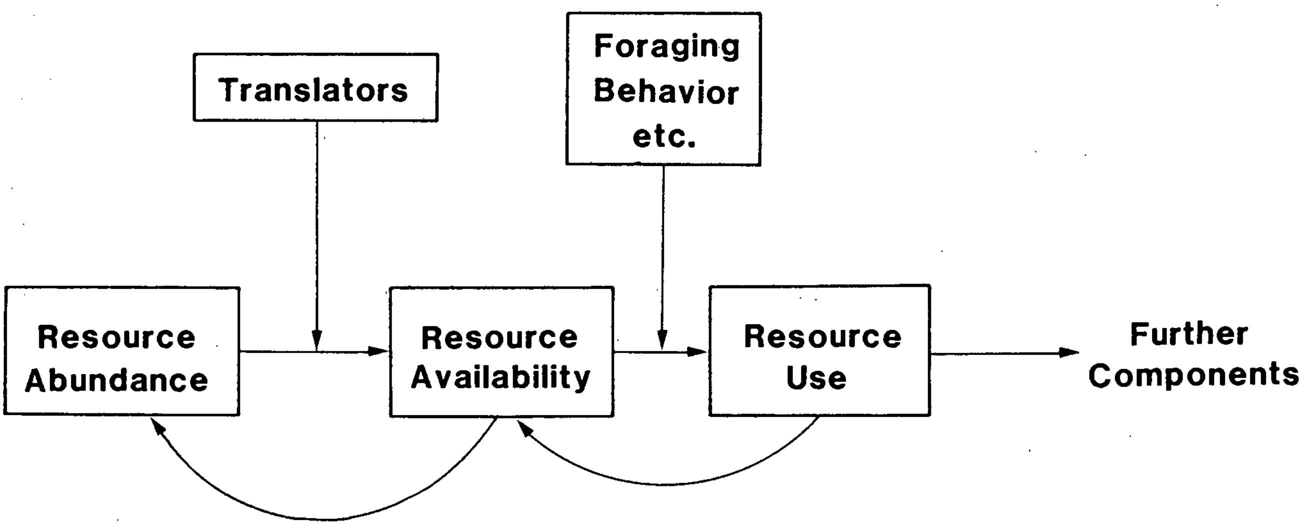

Figure 3.16. Initial components of resource systems and factors affecting the flux of resources between them (after Wiens 1984).

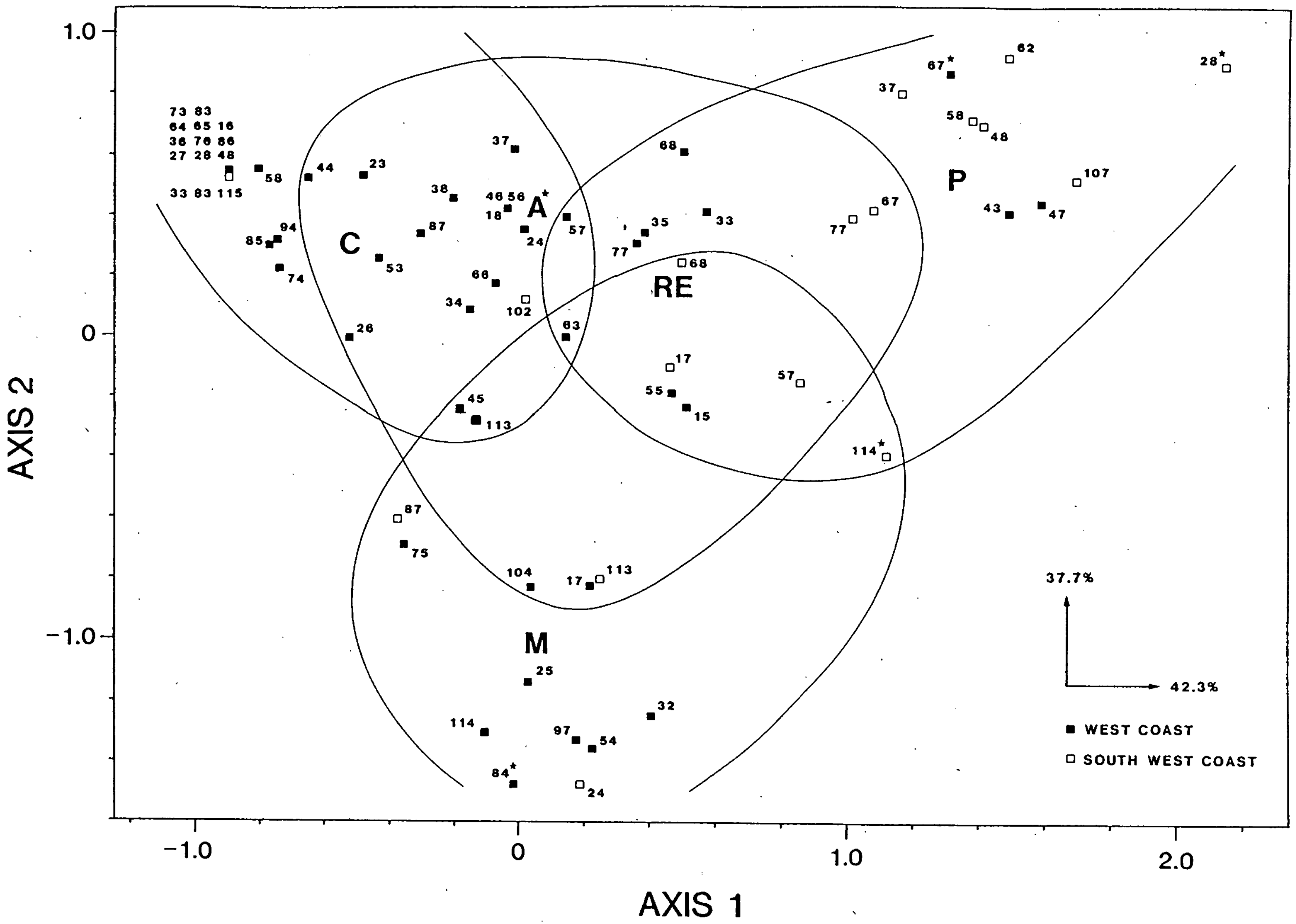

Figure 4.1. A correspondence analysis plot showing the monthly prey species composition of the diet of jackass penguins at the west and southwest coast during 1982–88. The first and second/third digit indicate(s) the month and the year, respectively. Asterisks indicate supplementary points. The prey species composition profiles of penguin diet in October 1987 at the west coast, and July 1984 at the southwest coast, are coincident with the origin.

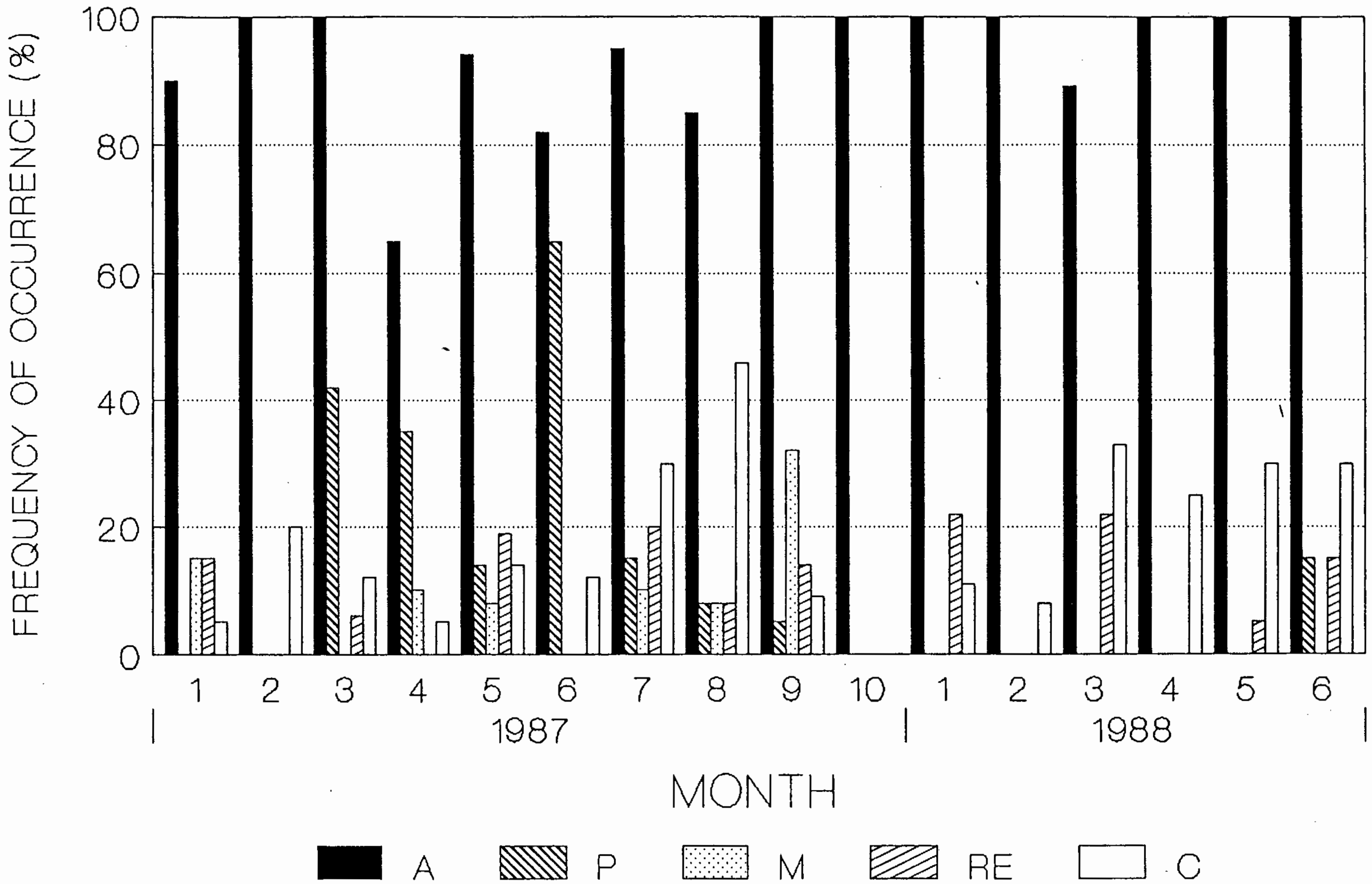

Figure 4.2. Monthly frequency of occurrence of anchovy (A), pilchard (P), maasbanker (M), red-eye (RE) and cephalopods (C) in the diet of west-coast jackass penguins during 1987-88.

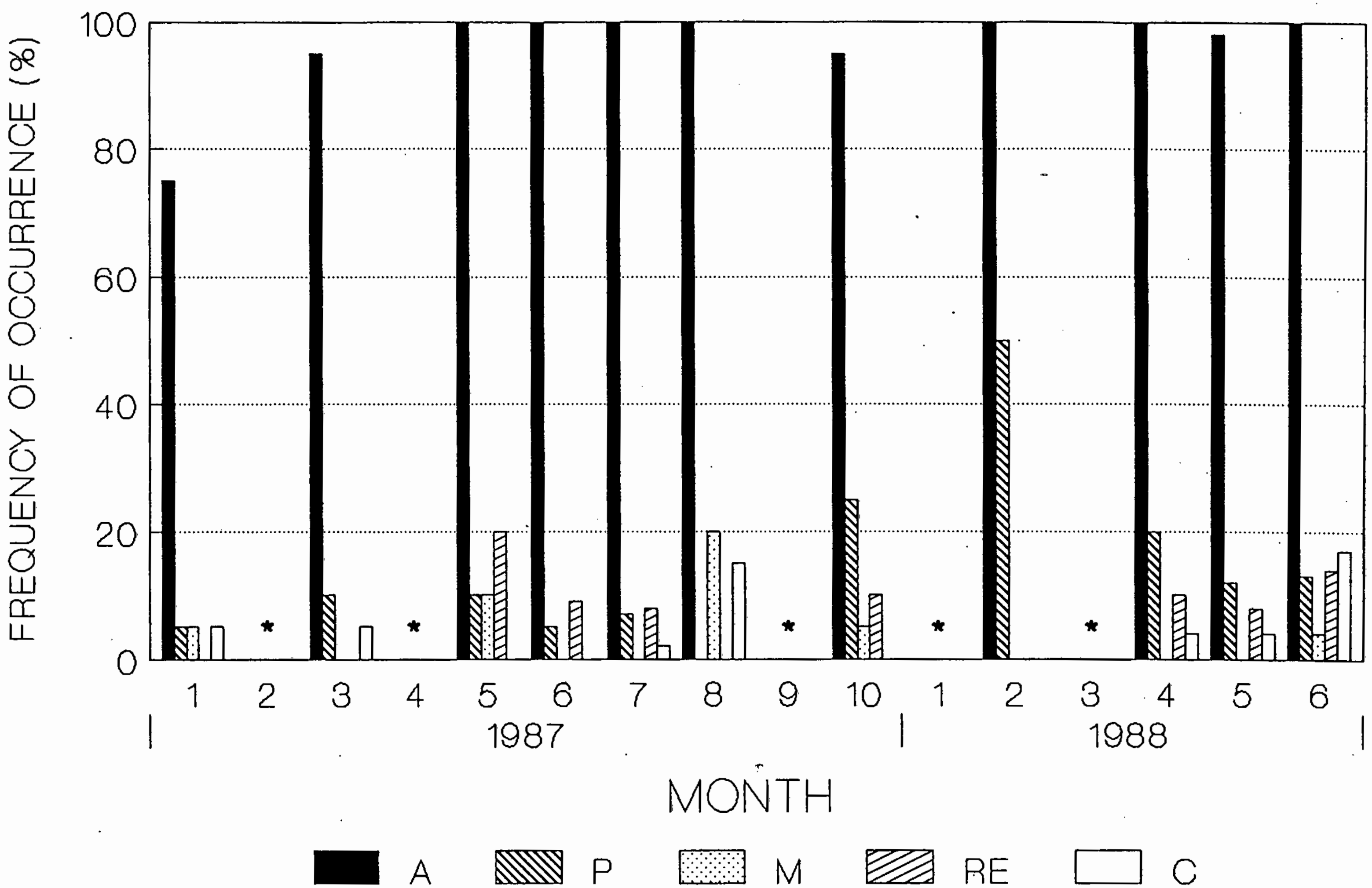

Figure 4.3. Monthly frequency of occurrence of anchovy (A), pilchard (P), maasbanker (M), red-eye (RE) and cephalopods (C) in the diet of southwest-coast jackass penguins during 1987-88. Asterisks indicate months in which no diet samples were collected.

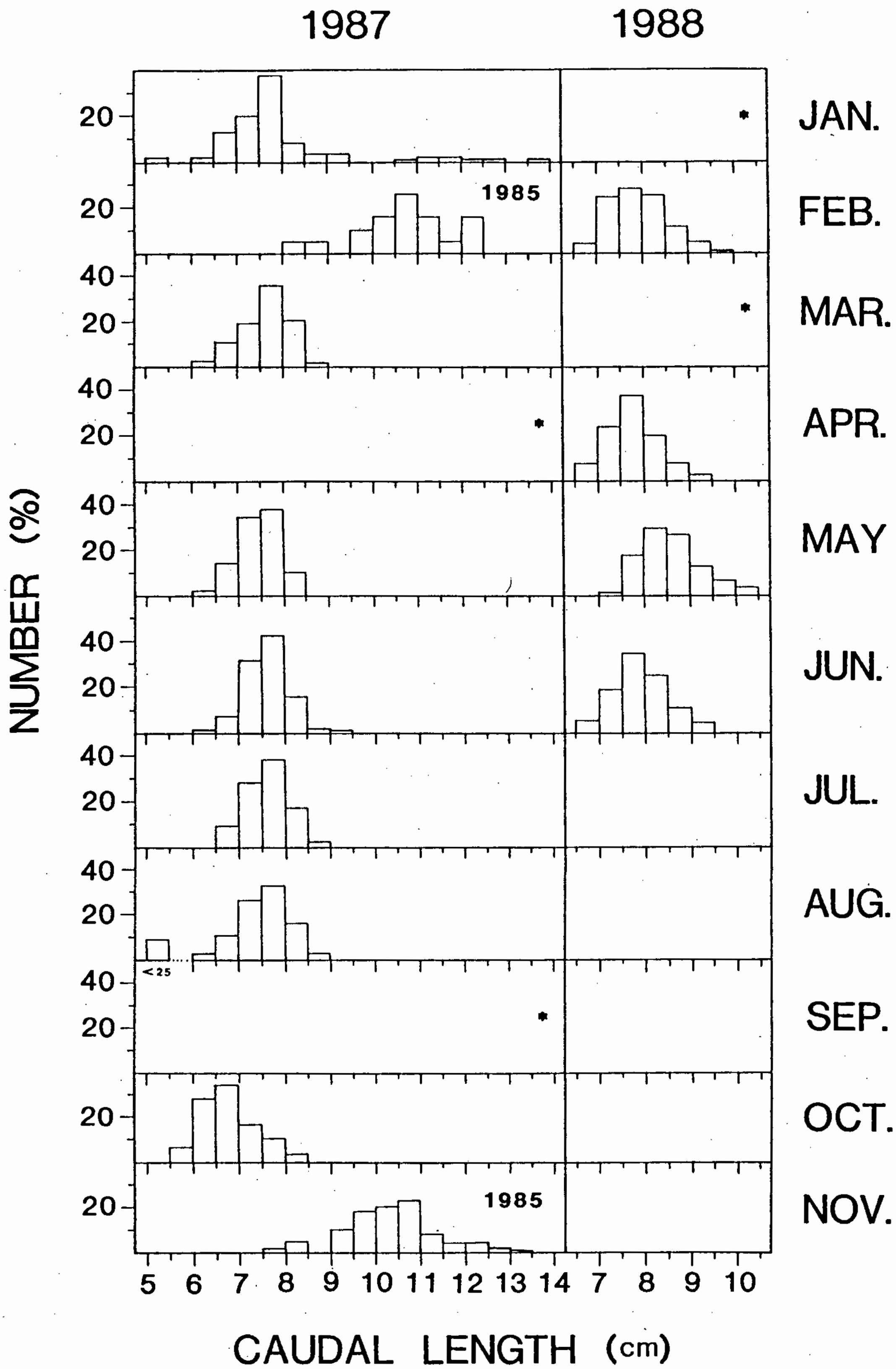

Figure 4.5. Monthly size-frequency distributions of anchovy in southwest-coast jackass penguin diet between 1985-88. During 1986, and in months of 1985 other than indicated, penguin diet was not sampled. Asterisks indicate no data.

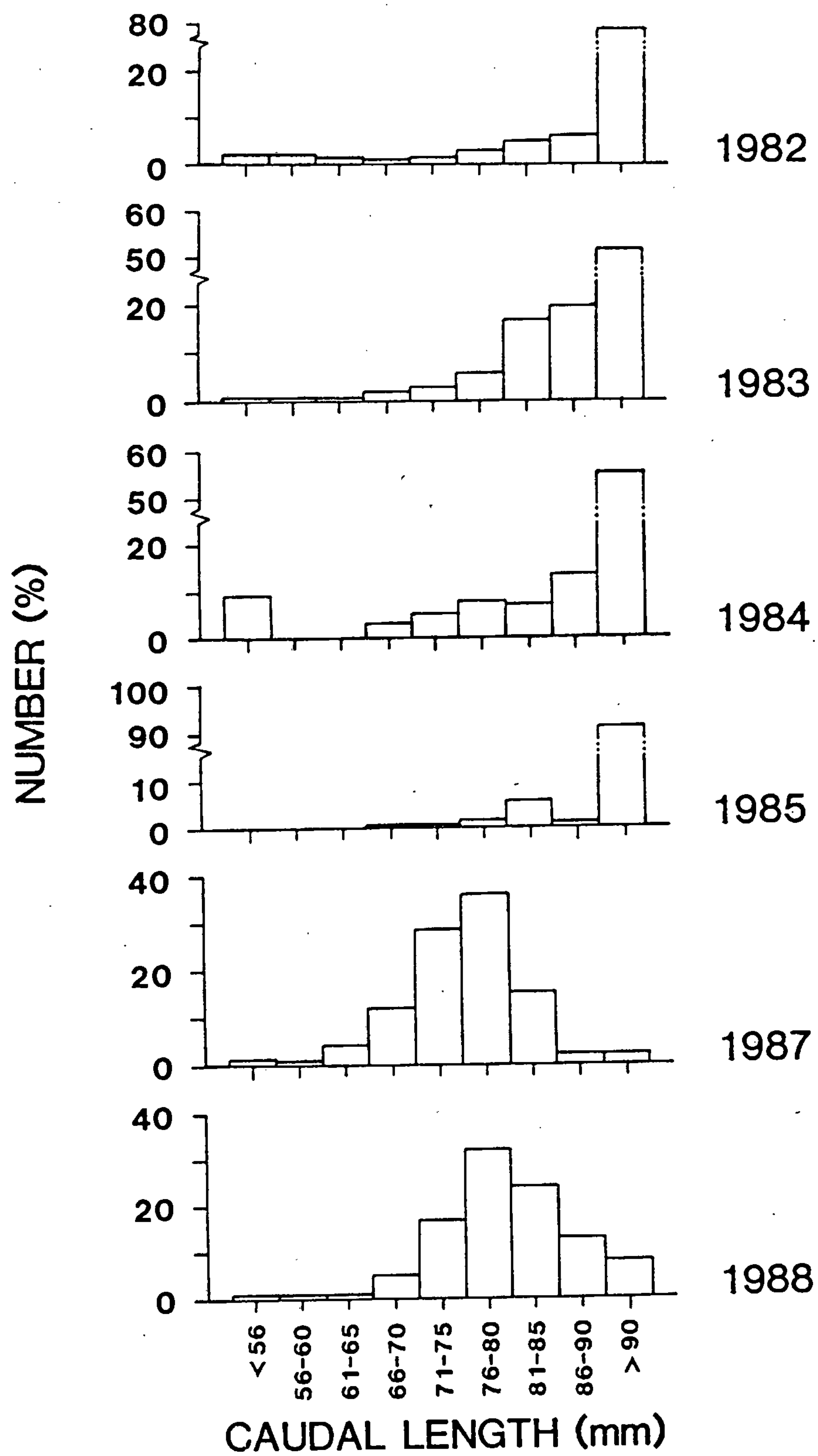

Figure 4.6. Annual size-frequency distributions of anchovy in southwest-coast jackass penguin diet between 1982-88. No data exist for 1986.

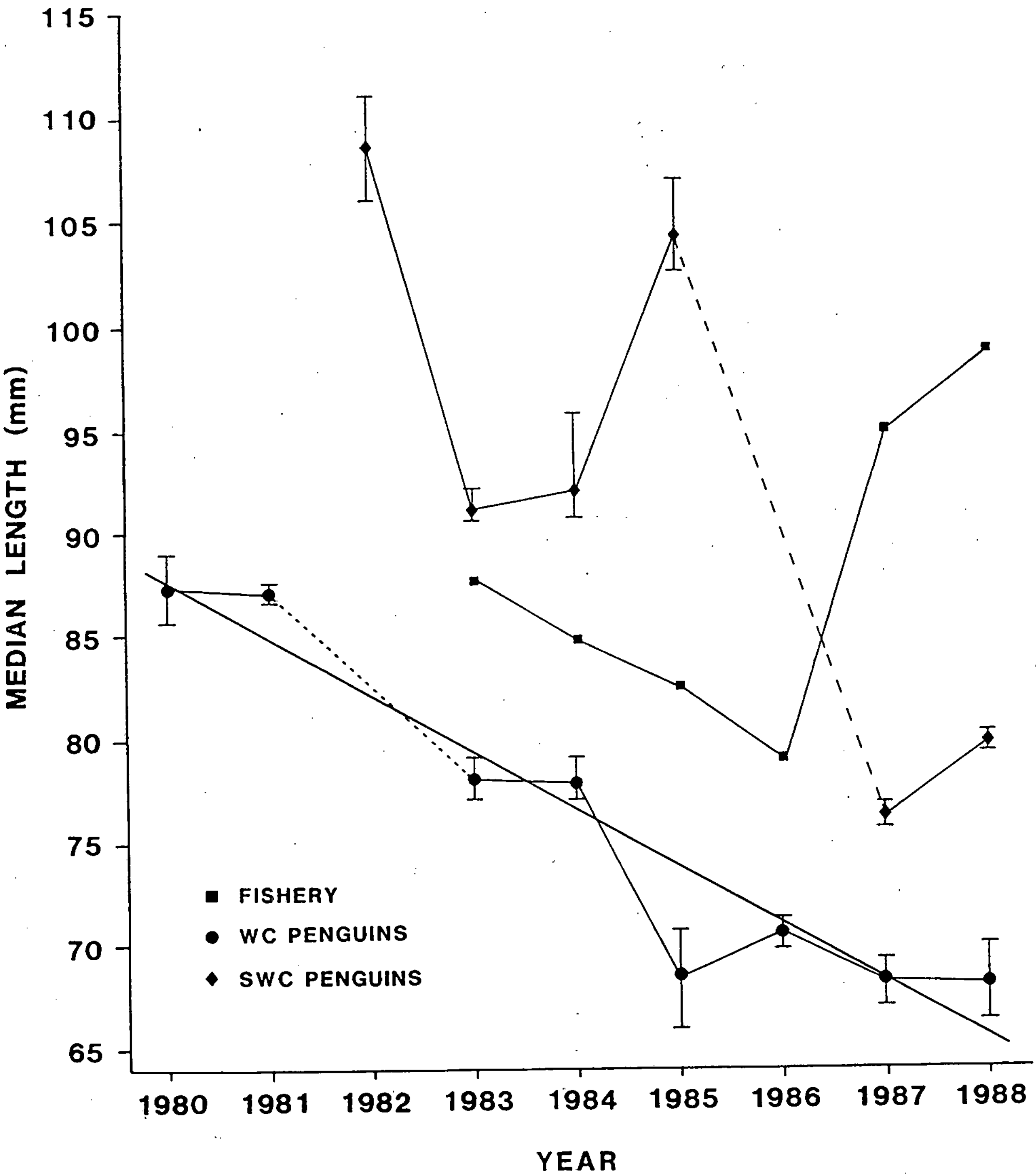

Figure 4.7. Annual median caudal length of anchovy in southwest- and west-coast jackass penguin diet and total South African purse-seine fishery catches between 1982-88, 1980-88 and 1983-88, respectively. Vertical bars represent the ≥ 95 % confidence interval around median lengths.

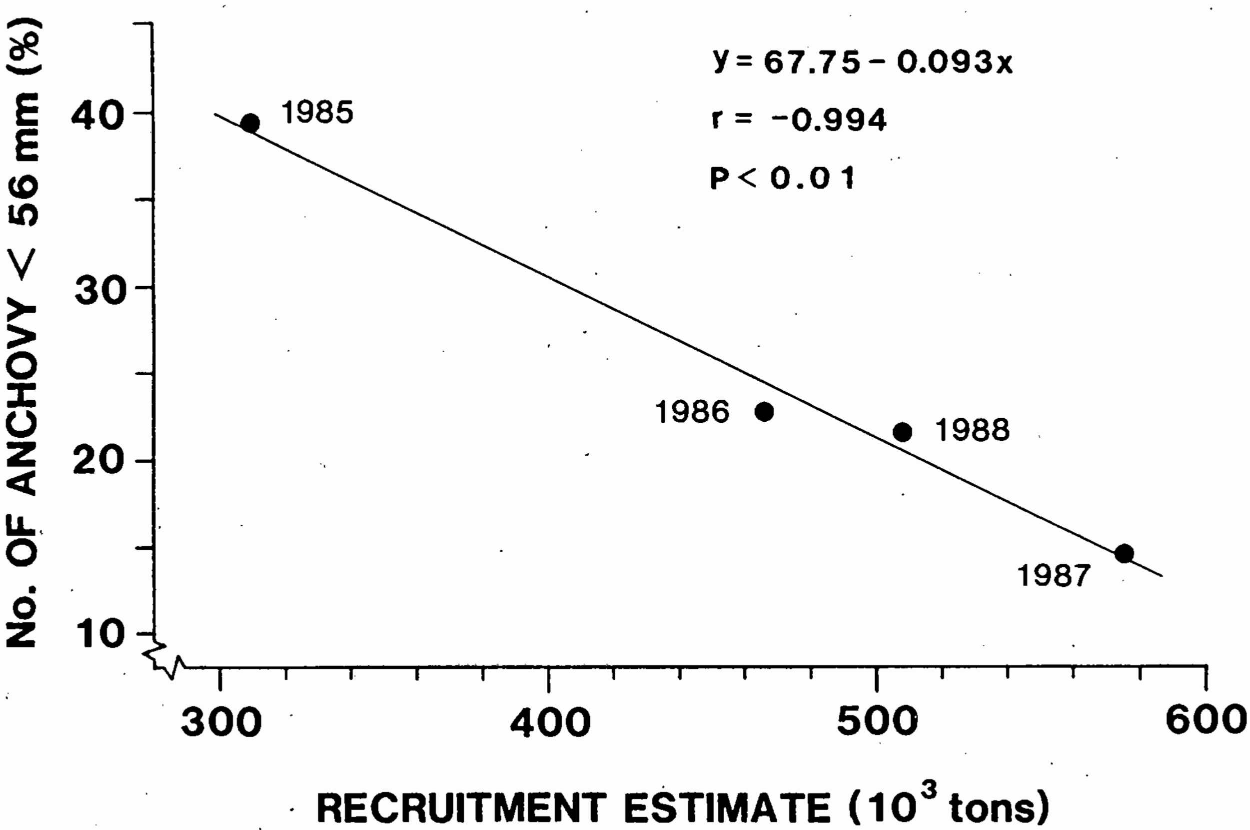

Figure 5.1. Correlation between the proportion of small anchovy (< 56 mm in caudal length) in west-coast penguin diet during January - July, and acoustic recruitment estimates of anchovy ($P < 0.01$).